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ATLAS OF ELAPID SNAKES OF AUSTRALIA

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21 AUG 1986
NATURAL HISTORY

ATLAS OF ELAPID SNAKES OF AUSTRALIA

Edited by Richard Longmore

Bioclimatic Analysis by John R. Busby

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Cover photograph
Parademansia microlepidota, Australia's deadliest elapid - Morney Plains, Qld (R. Jenkins)

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Foreword

The *Australian Flora and Fauna Series* comprises occasional publications designed to make available, as widely as possible, the results of biogeographical activities and projects undertaken by, or on behalf of, the Bureau of Flora and Fauna.

This seventh number deals with the distributions of members of the snake family Elapidae in Australia. The work maps actual localities by latitude/longitude and indicates a bioclimatic prediction range for each species.

Bureau of Flora and Fauna
June 1986

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ATLAS OF ELAPID SNAKES OF AUSTRALIA

21 AUG 1986

INTRODUCTION

This *Atlas* contains a map for each member of the snake family Elapidae found in Australia. The family contains all of the front-fanged, venomous, terrestrial snakes in Australia, representing some 77 species. Several of the world's deadliest snakes belong to this family, which has representatives in Africa, Asia, India, the Americas and the Pacific islands. The family reaches its greatest diversity in Australia. There are almost 17000 records contained in the *Atlas*. Each record is supported by an actual specimen held in one of the contributory institutions.

The concept of an atlas of the elapid snakes of Australia dates from late 1982 after records from the Australian Museum were used in a pilot project. A workshop on a reptile and amphibian atlas of Australia held at the Bureau in April 1983 commended the idea of producing atlases based on specimen records as it was considered wasteful to attempt to collect new field records without first utilising data already held by museums.

Elapids were confirmed as a suitable group to begin mapping because: i) the Bureau had already commenced to collect geographic elapid data from several museums as part of ABIS (Australian Biological Information System), ii) there were benefits to the community in mapping this group of venomous snakes and iii) it was a group from which results might be obtained in a relatively short time scale.

Museums and other institutions holding substantial collections of elapid snakes, both in Australia and overseas, were contacted, and the following contributed records:-

American Museum of Natural History (AMNH)
Australian Museum, Sydney (AM)
Australian National Wildlife Collection CSIRO (ANWC)
Australian National University Zoology Department, Canberra (ANUZ)
British Museum (Natural History) (BMNH)
California Academy of Sciences (CAS)
Central Australian Wildlife Collection, Alice Springs (CAM)
Chicago Field Museum of Natural History (Hosmer collection) (FMNH)
Conservation Service, Department of Territories Canberra (ACT)
Museum of Comparative Zoology, Harvard (Loveridge collection) (MCZ)
Museum of Victoria, Melbourne (NMV)
National Parks and Wildlife Service, Tasmania (TAS)
Northern Territory Museum of Arts and Sciences, Darwin (NTM)
Private collection, Dr. G. Mengden (GMP)
Queensland Museum, Brisbane (QM)
Queen Victoria Museum and Art Gallery, Launceston (QVM)
South Australian Museum, Adelaide (SAMA)
Tasmanian Museum and Art Gallery, Hobart (TMH)
Western Australian Museum, Perth (WAM)

The *Atlas*, with 17000 records, represents one of the largest documented records of an Australian animal taxon. The gathering of this volume of data was not always without problems. It is fair to say that collections held by several institutions were in a poor state of curation at the time of request. Misidentifications, loss of specimens and spurious localities resulted in many specimens having to be painstakingly verified by curators. Where latitudes/longitudes were not listed on specimen labels these had to be exhaustively determined, either by the various contributing institutions or, in the majority of cases, by the Bureau of Flora and Fauna. Where possible, all doubtful records were sent back to curators for final verification and all results failing to survive the rigorous checking process were deleted from the *Atlas* data base. Final data reflect identifications provided by institutions.

The nomenclature for the *Atlas* follows that of the *Zoological Catalogue of Australia, Vol. 1 Amphibia and Reptilia* by Cogger, H.G., Cameron, E.E. & Cogger, H.M. This catalogue, the first in a series of books aimed at covering the complete Australian fauna, was in preparation at the time the *Atlas* was initiated. Several alternative nomenclatures exist and are at variance in some instances with the names used in the *Atlas*. Storr, Smith & Johnstone (1986) and Wells & Wellington (1984, 1985) provide alternative nomenclatures in many instances. A particular example is the argument by Covacevich *et al.* (1981) and others, eg. Wallach (1985), for the placement of *Parademansia* in *Oxyuranus*. The *Atlas* is not intended to serve as a nomenclatural adjudicator but rather as a stimulus to further research on the distribution of these species. In the majority of cases where alternative nomenclature has been proposed, the specific epithet remains unchanged. It is acknowledged that there will always be room for debate in deciding generic placement. Two species of elapid have been described since Vol. 1 of the *Zoological Catalogue* was published, *Pseudechis butleri* Smith, 1982 and *Denisonia ordensis* Storr, 1984. Records from the Western Australian Museum have enabled these two species to be included in the *Atlas*.

Predicted distributions of each species were calculated using climatic data. In order for this bioclimatic prediction (BIOCLIM) to be determined it was necessary to assign elevations to all locality records included in the *Atlas*. As this information is not normally included in the specimen data supplied, elevations to the nearest 50 m were ascribed by the Bureau to each record. These were determined by examining contour gradients on 1:100 000 and 1:250 000 maps. Extremes were purposefully avoided.

The known distribution of each species is depicted by red asterisks, plotted from the latitude-longitude references (in degrees and minutes) for every specimen record. Predicted distributions, based on climatic similarities with actual localities as calculated by the BIOCLIM system (see Nix, this volume), are shown for all but three (rare) species. Predictions are on an Australia-wide half-degree latitude-longitude grid and are shown at two levels: the plus symbols indicate grid points where all climate parameters fell between the 5 and 95% values of the species' climate profile (see Appendix 3), and the dot symbols indicate points where all the parameters fell within the total range. No symbol was plotted where any climate parameter for a point fell outside the total range for the species. The total number of specimens plotted is indicated on the bottom of each map.

It is apparent from these data that many species are poorly represented in collections and as such the distribution map must be regarded as preliminary in nature. Members of the genus *Pseudonaja* represent 27% of the total number of specimens included in the data bank and examination of the maps for these species indicates their wide distribution on the mainland.

There are many other interesting points to note in examining the maps. The genus *Acanthophis* occurs throughout the greater portion of the mainland: a tropical northern species, a central desert species and a southern temperate species. Distinguishing the northern *A. praelongus* from the southern *A. antarcticus* has presented problems to many herpetologists and further detailed studies may show that many *A. antarcticus* records are in fact *A. praelongus*. The genus *Notechis* currently is treated as two species in Australia, however, these merge in South Australia where a confusing array of different morphs makes accurate determination difficult and points to the need for clarification of the number of species and species boundaries in this complex. Several genera, *Elapognathus*, *Neelaps* and *Rhinoplocephalus* are found only in Western Australia. Members of the genus *Simoselaps*, small, beautifully-marked, burrowing elapids, have radiated throughout the mainland, but display their highest level of diversity in the western portion of the mainland.

In order to enrich the maps, several Australian scientists were invited to contribute biogeographical essays. I am pleased that Henry Nix, Harold Cogger and Jeanette Covacevich were able to contribute.

Appendix 1 shows the total number of collecting sites for all specimens contained in the *Atlas*. It is obvious from this which areas are poorly represented in collections of elapid snakes. Major cities are highlighted and main roads, especially in country areas, stand out. Appendix 2 illustrates actual versus predicted species densities using 1:250 000 grids. Colours highlight predicted numbers and contrast areas of low and concentrated elapid densities. Appendix 3 lists the complete BIOCLIM species profile of each species (except three rare species) for all twelve environmental parameters used. These data provide supporting evidence to bioclimatic ranges.

This *Atlas* is, by its very nature, preliminary. It is certain that misidentified specimens have escaped the rigours of the checking processes and so have introduced errors into the system. This I feel is unavoidable, considering the size of the undertaking and the number of specimens and people involved. Information, including museum registration number, on any individual data point included in the *Atlas* can be obtained from the Bureau's Elapid Atlas data bank by contacting the Bureau. This data bank will be updated from time to time, enabling maps reflecting current knowledge to be produced. Individuals and government agencies are encouraged to contact and collaborate with museum authorities by providing additional records to determine more precisely the distribution of elapid species. I hope that the *Atlas* stimulates interest and research aimed at unravelling problems inherent in several of the maps. The Bioclimatic Prediction System will similarly, I hope, stimulate keen, active herpetologists to venture out in the field to corroborate BIOCLIM predictions. If we can validate even one unexpected but predicted site then it has been worth the effort.

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It would not have been possible to contemplate such an enormous venture as the *Atlas* without the cooperation, eagerness and kindness of many people, especially:-

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Richard Longmore
Editor

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A BIOGEOGRAPHIC ANALYSIS OF AUSTRALIAN ELAPID SNAKES

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INTRODUCTION

Although basic concepts and methodology had been developed and tested some years earlier, the present BIOCLIM package, complete with operating manual, became accessible to users throughout Australia on CSIRONET in January, 1984. Since then, the number, range and variety of applications have been gratifying, but this *Atlas of Elapid Snakes of Australia* is the first major application of this new technology. Although designed to exploit the latent potential of specimen label information in museum and herbarium collections, BIOCLIM can be used for analysis of any set of point-based records or observations.

Potential users must understand the underlying concepts and be aware of inherent limitations in the current BIOCLIM package. This *Atlas* provides an appropriate vehicle for discussion of both the potential of and problems in using BIOCLIM for taxonomic and biogeographic analysis. That BIOCLIM predicts potential distribution *solely on the basis of bioclimate* must be emphasised. This provides a first approximation to limits of distribution, but obviously other environmental factors and interactions will influence actual distribution. Further development of the system aims at incorporating additional key environmental attributes and derivation of more comprehensive indices.

BIOCLIM: POTENTIAL AND LIMITATIONS

While BIOCLIM does have a very wide range of potential applications in taxonomy, biogeography and ecology, users must be made aware of a number of factors that will determine the quality and value of the output. The most important of these factors are listed and discussed using examples drawn from this *Atlas*.

1. Error associated with estimation of primary climatic attributes at a point

Long-term monthly mean values for precipitation and maximum and minimum temperature are estimated at any point in Australia given position (latitude and longitude) and elevation. The surface-fitting procedure is empirical and uses Laplacian smoothing splines with generalised cross validation (Wahba & Wendelberger, 1980) and was first tested and applied to estimation of continental-scale climatic data in a study of mean daily global solar radiation for Australia (Hutchinson *et al.*, 1984). Estimates of monthly mean maximum and minimum temperature are based on a network of almost 1000 stations while estimates of monthly mean precipitation are based on a network of more than 15000 stations. Predictive error is generally less than 10 per cent for monthly precipitation values and less than 5 per cent for mean maximum and minimum temperatures. Where climatic gradients are steep and/or complex and sampling inadequate (*i.e.* sparse network) this error term may be higher.

Further development of these and additional climate surfaces is proceeding, but significant improvement will depend on upgrading of existing networks and physical modelling of terrain/climate interactions. Even so, extensive development and testing of the precipitation and temperature surfaces currently incorporated in BIOCLIM indicate that predictive error is of about the same magnitude as normal instrumental and observer error. Thus, these estimates of primary climatic attributes are generally robust and the least likely cause of anomalous values in the analyses that follow.

2. Relevance of derived bioclimatic indices

Initially, for each point, BIOCLIM generates 36 primary climatic attributes (12 monthly mean values for each of precipitation, maximum and minimum temperature). From these attributes are derived a set of indices that are considered to have biological significance and that summarise annual and seasonal mean conditions, extreme values and intra-year seasonality. Ideally, key terms in the dynamic energy and water balances should provide indices with greatest generality. In the absence of these terms it becomes necessary to use surrogate terms derived from the available precipitation and temperature estimates. Thus, for example, annual mean temperature and annual mean precipitation provide a gross approximation of total energy and water inputs at a site. Highest and lowest monthly mean values provide a measure of seasonal extremes and allow computation of annual range. Mean temperature and precipitation of wettest and driest successive three month periods (wettest and driest quarter) provide a measure of conditions prevailing during potentially active and dormant seasons.

The initial set of 12 bioclimatic indices incorporated in BIOCLIM and used in production of this *Atlas* is:

(1) annual mean temperature (°C);

(2) hottest month mean maximum temperature (°C);

(3) coldest month mean minimum temperature (°C);

(4) annual temperature range (2 minus 3)(°C);

(5) wettest quarter mean temperature (°C);

(6) driest quarter mean temperature (°C);

(7) annual mean precipitation (mm);

(8) wettest month mean precipitation (mm);

(9) driest month mean precipitation (mm);

(10) annual precipitation range (8 minus 9) (mm);

(11) wettest quarter mean precipitation (mm); and

(12) driest quarter mean precipitation (mm).

Essentially, the bioclimatic indices describing the temperature and water regimes are in parallel and equally balanced. While there are strong and often linear correlations between these indices within localised regions, these correlations tend to break down at continental and sub-continental scales. Experience has shown that each of these 12 indices can provide useful discrimination in particular applications, but that additional indices may be needed for more complete circumscription of the bioclimatic envelope.

An example of limitations imposed by use of the standard 12 bioclimatic indices is provided by the *Atlas* map for *Echiopsis curta* (Map 26). The specimen-based distribution is centred on winter-wet, summer-dry environments of southern Australia extending from the SW of W.A. through the Eyre Peninsula to the Murray Mallee of S.A. and adjacent areas of Vic. and N.S.W. The *predicted* potential distribution, however, includes outlying points in south-central Qld. This is the result of inadequate definition of precipitation and temperature seasonality by the original 12 indices. Addition of more explicit terms for seasonality resolves these problems. Either annual range divided by monthly mean or the coefficient of variation of both monthly temperature and precipitation values are effective indices.

In southern Australia, where the wettest quarter is in winter when temperatures are limiting for biological activity, additional discrimination is provided by adding mean temperature and precipitation for warmest and coldest quarters. A measure of isothermality (mean diurnal range/mean seasonal range) provides useful discrimination for tropical, insular and maritime environments. Addition of these indices to the original 12 bioclimatic indices improves description of bioclimatic regimes and minimises anomalies in predicted potential distributions.

3. Derivation of the bioclimatic envelope

The procedure used in BIOCLIM for this *Atlas* is based on simple matching of selected thresholds and limits for each of the 12 bioclimatic indices across a grid of points used for predicting potential distribution. Cumulative frequency distributions of values for each bioclimatic index are plotted and inspected for evidence of significant departures from normality. Following checking of anomalous data points and corrections where necessary, the upper and lower limits and the 5, 25, 50, 75 and 95 percentile values for each of the 12 indices provide the basis for the bioclimatic envelope or taxon template. Core and marginal environments can be estimated using selected threshold values for all 12 or some selected subset of the indices.

For this *Atlas*, core environments are those whose values fall within the 5 and 95 percentile range for all 12 of the bioclimatic indices and marginal environments are those in which values fall outside this range for one or more of the indices, but within the upper and lower limits. While these limits are arbitrary, they are explicit. The advantages of this procedure lie in its simplicity and in the fact that the indices used do have physical meaning and can be used directly in interpreting biological responses. Disadvantages lie in the lack of consideration of possible interactions and partial substitutions *e.g.* lower rainfall at a site may be compensated by lower potential evaporation reflected in lower temperatures.

Use of a large number of bioclimatic indices is advantageous because this minimises the problem of defining over-generous limits to predicted potential distributions. This problem arises because only a subset of all possible combinations of bioclimatic indices will occur *e.g.* a taxon may occur at a site close to the lower limit for annual precipitation, but only where annual mean temperatures lie close to their lower limit. In fact, the problem is minimised when the water regime is characterised by indices derived from a water balance rather than from precipitation values. The addition of more explicit seasonality and isothermality indices to the basic 12 indices used in this version of BIOCLIM significantly improves definition of the bioclimatic envelope and eliminates or reduces the incidence of spurious outliers in predicted distributions.

4. Accuracy and level of resolution of the grid used for predicting potential distribution

The bioclimate profiles are matched against a grid of data points that have climatic data. Thus, the profiles are matched against data from the existing network of climatic stations. Matching enhances accuracy since the climatic data are based on instrumental measurement, but spatial resolution is highly variable because of the non-regular distribution of climatic stations. A regular grid of climatic data points is preferable for spatial analysis and, in principle, can be generated at any desired level of resolution by coupling the climatic surfaces to a grid of elevation data. For continental scale analysis the grid used in BIOCLIM provides a resolution of 0.5° of latitude and longitude. The grid was derived by manual interpretation of elevations at grid intersections using best available maps.

Close inspection of the *Atlas* maps reveals that the 0.5° grid does not provide adequate resolution in mountainous and complex terrain. The fact that some maps display disjunct specimen records that fall outside the predicted distribution is due to the coarseness of the grid and not to problems in the mode of analysis. Obviously, the scale of final publication dictates the level of resolution that can be used and at the scale used for this *Atlas* the 0.5° grid is appropriate. Continued development of BIOCLIM aims at incorporating a grid with 0.02° resolution at continental scale which will be based on a digital elevation model derived from 1:100 000 map sources.

5. Versatility of graphic display and plotting procedures

Incorporation of the mapping package MAPROJ (Hutchinson, 1981) provides options for plotting distribution maps at any desired scale and projection. This feature is particularly valuable for plotting point data and/or predicted potential distributions as an overlay for some existing thematic map *e.g.* vegetation, soils, geology. Commercially available graphics packages can extend the system by generation of predicted potential distributions on a three dimensional plot of the land surface. Other options include use of a full colour range and very wide choice of symbols and shading or texturing.

The preceding five factors relate to integral components of the total system and for most users of BIOCLIM are not readily amenable to user control. Options, however, do provide access to outputs at various steps in the total procedure, giving specialist users the opportunity to explore alternative methodologies. The second set of five factors is very important in determining the quality of output and is much more subject to user control.

6. Taxonomic uncertainty

Biogeographic analysis can proceed at any one of a number of taxonomic levels, but in this *Atlas* the operational taxonomic unit is the species. Despite recent focus on the taxonomy of Australian Elapidae it is clear that much uncertainty remains. Cogger (1975, 1979) stated that the existing classification was uncertain and unreliable and that most species were probably composite. Schwaner *et al.* (1985), Wallach (1985) and Mengden (1985a,b) used modern methods of immunological, chromosomal, electrophoretic and cladistic analysis in attempts to clarify the taxonomic status of the Australian Elapidae. Much of this work is concerned with higher order taxonomic groupings which will no doubt lead to generic name changes and regroupings, but this is not of primary concern for the *Atlas.* What is of concern is the possibility of composite species. Thus, within the currently recognised genus *Pseudonaja,* Wallach (1985) notes that *P. affinis* is possibly two species and Mengden (1985) states "the composite nature of *P. nuchalis* is not yet resolved, but available electrophoretic data are concordant with chromosomal data and strongly support the conclusion that there exist at least three distinct species within what is currently known as *P. nuchalis".*

The value of bioclimatic profiling and of any mapped distribution or biogeographic analysis that flows from it, is very much dependent on the taxonomic integrity of the target taxa. Some of the problems are well illustrated in this *Atlas.* Differing concepts of museum curators in circumscribing members of the *Notechis* tiger snake complex has led to the preparation of separate maps for *N. ater* (Map 40), *N. scutatus* (Map 41) and one for all records of *Notechis* species (Map 42) from this complex (see comments in Introduction).

7. Accuracy of identification and labelling

The level of curatorial treatment varies greatly from institution to institution and within institutions from one taxonomic group to another. Not infrequently, old specimens are misidentified and/or mislabelled. The BIOCLIM analysis has proven to have considerable value in identifying anomalies *i.e.* specimen records that produce extreme values in the bioclimatic profile of a taxon. This is particularly the case when a map plot of distribution indicates nothing abnormal. In most BIOCLIM runs for a target taxon, the initial run commonly reveals anomalies which require further checking of specimens held in collections. This was the case in many instances in the *Atlas.* In some cases the cumulative frequency curves for bioclimatic indices may display bimodal or more complex distributions. This may be due to inadequate sampling, but can indicate that two or more components have been included within the named taxon.

8. Accuracy of geocoding

Despite the evident problems, experience has shown that an acceptable level of geocoding can be derived retrospectively. Intelligent use of modern 1:100 000 or 1:250 000 topographic maps coupled with verbal descriptions of collecting sites on specimen labels or in field notebooks can yield satisfactory geocodes. Where climatic gradients are relatively gradual, as they are for much of Australia, a location error of ± 10′ of latitude and longitude and of ± 100 m elevation will not significantly affect the estimates of basic climatic attributes. Much more precision is needed in mountainous and hilly terrain, where location should be specified at better than ± 5′ and elevation at better than ± 50 metres. Where insular or maritime influences or scarp induced windward and leeward effects are important then location should be specified at ± 1′ and elevation at better than ± 20 metres. Wherever the location, at all times, geocoding should be made at the highest level of precision possible. While current climate surfaces may not warrant geocoding at such a high level of precision, developments in the near term future will.

The maps in this Atlas are based on the examination of more than 17000 specimen records and the geocoding of almost 16000 of these records, principally by Mr R. Longmore of the Bureau of Flora and Fauna. Once again, BIOCLIM analysis commonly revealed anomalous location records because of extreme values in the bioclimatic profile of a taxon. In fact, BIOCLIM analysis forms an integral and recursive component of the data checking process.

9. Adequacy of point sampling within total distribution

Most collections, and those of elapid snakes in particular, have been opportunistic. Very large numbers of specimens originate close to large centres of population. Thus, for example, there are very large numbers of specimens of *Demansia psammophis* (Map 13) collected within the vicinity of Perth, Sydney and Brisbane. The same phenomenon of large collections close to centres of human population can be observed in most of the maps in this *Atlas*. Also evident in the maps is the fact that collectors tend to travel along roads and, particularly in an earlier era, railway lines (Appendix 1).

Obviously such bias in sampling presents problems for conventional modes of statistical analysis. In particular, the sampling bias poses problems for calculation of highly desirable probability density functions. One possible solution is to re-sample using a grid and simple presence/absence data rather than total number of specimens. The simple matching procedure used in BIOCLIM avoids many of the problems associated with geographic bias in sampling.

Firstly, the method involves separate matching of a large number of indices (12 in this case) estimated at each site. Threshold values are based on the outer limits of each distribution (5 and 95 percentile values and upper and lower limits) rather than on the central tendency. Where very large numbers of specimens have been collected within a relatively circumscribed region there is a redundancy of bioclimatic information. On the other hand, single specimens collected at or near the limits of distribution yield valuable bioclimatic information. The fact that specimens have been collected along roads and railway lines need not present problems providing that major bioclimatic gradients have been sampled.

Over time, as taxonomic uncertainty is reduced and distributions become better known, there is a tendency to collect more specimens at the margin. This is because the presence of a taxon is recognised as being unusual *i.e.* outside the known range. Problems remain with recently recognised and poorly collected taxa and these are most obvious when the few specimens known are from the vicinity of a single type locality. In such cases an alternative mode of analysis could be used in which an association or similarity measure could be calculated for the type locality against all other points on the grid and selected threshold levels of bioclimate similarly plotted.

10. Checking of anomalous data points

The use of cumulative frequency curves for identification of potential anomalies is an important component of the BIOCLIM analysis. Its role in locating possible misidentification, mislabelling and geocoding errors and in drawing attention to possible taxonomic anomalies has been described earlier. Given the extremely variable level of sampling of distributions there is difficulty in setting firm rules, but the upper and lower limiting values of each of the bioclimatic indices are worth checking as a matter of course. Where a number of limits coincide at a single specimen location, this coincidence is worthy of more detailed checking.

For some users potential anomalies only become evident when points are plotted on a distribution map. Points can be deceptive as genuine disjunct distributions occur. For example, the northernmost population of *Notechis scutatus* (Map 41) in the Carnarvon Ranges of central Queensland is widely separated from the main populations to the south, yet the bioclimatic profile of the Carnarvon Ranges population conforms with requirements for the core distribution. Further extreme outliers that are predicted in north Queensland at elevations exceeding 900 m on mountains and inland basalt tablelands conform only with the marginal distribution limits and must be regarded as having a lower probability of occurrence.

BIOGEOGRAPHIC ANALYSIS

The concept of zoogeographic sub-regions for Australia has a long history of development and use and undoubtedly has some heuristic value. Most proposals have been variations on the original theme of Baldwin Spencer (1896) who divided the continent into a northern, higher rainfall Torresian Zone, a southern and southeastern higher rainfall Bassian Zone and an arid interior Eyrean Zone. These reflect the major climatic controls operating over the continent and, therefore, it is not surprising that the Spencerian system has persisted for so long. Problems however arise when attempts are made to quantify the basis for regionalisation and to generate finer subdivision and more explicit definition of boundaries.

The first attempt to provide a more quantitative basis for zoogeographic regionalisation was that of Kikkawa & Pearse (1969) who used methods of numerical taxonomic analysis on presence/absence data for bird species at sample locations across the continent. More recently, Cogger & Heatwole (1981) used numerical taxonomic analysis to analyse the distribution of component species of six families of Australian reptiles in 100 sample plots based on a 1° grid of mainland Australia and Tasmania. The methods used in both of these studies allocate sample locations to exclusive groups and generate discrete boundaries.

The bioclimatic profiles that are output from BIOCLIM provide a quantitative description of the bioclimatic environment occupied by a given species as determined by actual specimen locations. In the following biogeographic analysis, numerical taxonomic procedures were used to classify taxa in terms of the similarity of their bioclimatic profiles; then new profiles were calculated for the derived groups and their distributions were plotted.

The classifications of those elapid taxa with sufficient data for analysis (73 species) were based on 38 bioclimatic attributes. These attributes were: the mean, upper and lower limiting values for each of the 12 bioclimatic indices, plus two seasonality indices (one for precipitation and one for temperature) computed using the mean values for monthly mean and annual range taken from each profile. Prior to classification, total annual precipitation and wettest quarter precipitation were transformed by taking their square root. This transformation reduces the influence of extremely high values and increases the level of discrimination at the low to moderate precipitation values that are characteristic of much of Australia. Using the Numerical Taxonomy Package or NTP (Belbin *et al.*, 1984) an hierarchical polythetic agglomerative strategy was used. An association measure that standardises attribute value by range (Gower metric) was generated (ASO) and used with the UPGMA Strategy in FUSE (Belbin, 1984) to generate a polythetic agglomerative fusion of elapid taxa.

Relationships between all 73 taxa are shown in the dendrogram (Figure 1). Three major groupings are evident and analysis of biogeographic pattern has been carried out at this three group level and, with further subdivision, at the ten group level. Recalculation of means and standard errors for each of these new groups took into account their differing sample sizes and permitted estimation of limits which enclosed 95 per cent of the total range of values for each bioclimatic attribute. These limits were matched against the grid to produce map plots of core bioclimatic environments and distributions for each group.

Essentially, at three group level, the maps of these core regions (Figure 2) are in accord with original Spencerian concepts although some boundaries differ significantly. The primary division separates a broad zone across northern and northeastern Australia from the remainder and this broadly approximates the classical Torresian zone. At the next division a core zone extending across southern Australia and well up the eastern coast approximates the Bassian zone. The northward extension of this zone as far as north Queensland reflects the influence of mountains and tablelands in moderating temperatures and closely parallels the Kosciuskan zone recognised by Kikkawa & Pearse (1969) in their biogeographic analysis of bird distribution. The third residual zone includes the classical Eyrean zone, but extends well beyond the limits that are normally recognised. Most of the southwest corner of Western Australia and much of east-central Australia is included. The means and standard errors of bioclimatic attributes for each of these three primary zones (Table 1) do indicate significant differences, but also illustrate the degree of overlap in values between groups. The fact that boundaries overlap, and thus are fuzzy and not discrete, will be evident also from inspection of the maps in Figure 2.

To gain additional insight it has been necessary to go beyond the data available in this analysis and consider measures available from a classification based on plant growth models (Nix, 1981, 1982). One measure that shows a close correspondence with the boundaries of this third continent-wide zone is the mean duration of soil profile saturation as determined from a water-balance. Essentially, the elapid snake taxa centred in this zone (49 species) do not occur where the mean duration of soil profile saturation exceeds three months each year. The single exception to this boundary condition is in the southwest of Western Australia, where the presence of extensive areas of sandy, free-draining soils alleviates waterlogging and possibly favours extension of the distribution of more arid adapted species into higher rainfall zones.

At the ten group level (Figure 3), the continent-wide Eyrean zone has five sub-regions, the southern and eastern Bassian zone three sub-regions and the northern Torresian zone two sub-regions. In each case these sub-regions reflect distinct bioclimatic environments that are occupied by a group of elapid snake taxa which have similar bioclimatic profiles. In many biogeographic zonations of Australia the southwest of Western Australia is recognised at four group level, but despite the presence of a number of endemic elapid taxa, the bioclimatic profile analysis does not support separation of this region at such a high level. In fact, the typical Mediterranean winter wet/summer dry environment does not separate until the eight group level. The core distributions of the ten groups are mapped and the means and standard errors of bioclimatic attributes listed for each group (Table 2). The sequence conforms with that of the dendrogram (Figure 1) with the first five groups forming sub-regions within the continent-wide Eyrean zone.

The first group comprises 17 species which have broad bioclimatic tolerances although not necessarily continent wide distributions. They are absent from the wettest and coldest regions. Within this large group, some species occur only in the east, see *Simoselaps australis* (Map 59), *Furina diadema* (Map 28), *Glyphodon barnardi* (Map 30) and *Unechis boschmai* (Map 69) while others occur only in the west, see *Demansia olivacea* (Map 11) and *Denisonia punctata* (Map 20). Some of the taxa with very wide distributions, see *Pseudonaja nuchalis* (Map 54), are almost certainly composite species. In one case, *Acanthophis antarcticus* (Map 1), the location data are known to relate to two species and many of the records from northern Australia refer to *A. praelongus* (Map 2).

The second group comprises 12 species that occur within the limits of the arid and semi-arid zones as normally defined and conforms with classical delineations of the Eyrean zone. Only one species *Acanthophis pyrrhus* (Map 3) is widely distributed throughout this sub-region, while others have extensive distributions either on the sandy substrates of the Western Shield, see *Simoselaps approximans* (Map 58), *S. anomalus* (Map 57), *Denisonia fasciata* (Map 17), *Pseudechis butleri* (Map 46) or on the cracking clays of the Mitchell grass plains across the north and in the east, see *Pseudechis colletti* (Map 47), *Pseudonaja guttata* (Map 51), *P. ingrami* (Map 52). One species, *Parademansia microlepidota* (Map 44), has the core of its distribution in the very arid Cameron's Corner region. This group is not well collected; six of the twelve species are represented by less than 50 specimens each.

The third group comprises five species that have their core distribution in central eastern Australia inland from the coastal ranges. Temperatures are lower than for the first two groups and driest quarter precipitation significantly higher. Two species, *Denisonia maculata* (Map 18) and *Glyphodon dunmalli* (Map 31), are restricted to the northern sector while the remaining three species, *Hemiaspis damelii* (Map 33), *Pseudechis guttatus* (Map 48) and *Unechis dwyeri* (Map 70), extend further to the south.

The fourth group comprises 12 species that have their core distribution within the Mediterranean winter wet/summer dry zone of southern Australia. All 12 species occur in the SW of Western Australia and six species are confined to this region, see *Drysdalia coronata* (Map 21), *Elapognathus minor* (Map 27), *Rhinoplocephalus bicolor* (Map 56), *Neelaps calonotus* (Map 39), *Unechis gouldii* (Map 72) and *Simoselaps littoralis* (Map 63). A further three species extend further eastward into South Australia, *Neelaps bimaculatus* (Map 38), *Pseudonaja affinis* (Map 50) and *Simoselaps bertholdi* (Map 60). The final three species range throughout the sub-region, see *Echiopsis curta* (Map 26), *Unechis nigriceps* (Map 74) and *Simoselaps fasciolatus* (Map 61). In addition, two of the species in this fourth group range well beyond the core zone into the arid zone proper, *Simoselaps bertholdi* and *S. fasciolatus.*

TABLE 1 Means and standard errors of 12 indices from the bioclimatic profiles of three primary zoogeographic regions of Australia

(A) Temperature based indices (units °C)

	Annual mean temperature	Min. temperature coldest month	Max. temperature hottest month	Annual temperature range	Mean temperature wettest quarter	Mean temperature driest quarter
1. 'Eyrean'	19.7±2.7	7.0±3.7	32.7±3.9	25.7±4.5	20.1±7.6	19.6±4.4
2. 'Bassian'	15.9±3.4	4.9±3.2	26.8±3.1	20.6±4.7	16.9±6.3	15.5±3.3
3. 'Torresian'	25.1±2.4	15.0±3.7	33.4±2.5	18.4±3.9	27.2±1.7	22.4±3.0

(B) Precipitation based indices (units mm)

	Annual mean precipitation	Precipitation wettest month	Precipitation driest month	Annual precipitation range	Mean precipitation wettest quarter	Mean precipitation driest quarter
1. 'Eyrean'	607±397	109±83	16±16	93±84	313±230	56±52
2. 'Bassian'	1076±419	148±85	46±17	102±74	413±230	156±56
3. 'Torresian'	1378±486	316±105	13±17	306±102	866±290	48±58

TABLE 2 Means and standard errors of 12 indices from the bioclimatic profiles of ten zoogeographic regions for Australia

(A) Temperature based indices (units °C)

	Annual mean temperature	Min. temperature coldest month	Max. temperature hottest month	Annual temperature range	Mean temperature wettest quarter	Mean temperature driest quarter
1. 'Eyrean'	20.5±3.9	7.3±4.2	33.3±4.0	26.0±4.7	21.9±7.3	19.2±4.5
2. 'Eyrean'	22.5±2.7	7.1±2.9	36.8±2.0	29.7±2.6	26.1±6.0	19.6±3.9
3. 'Eyrean'	18.1±3.6	3.6±2.7	31.5±2.5	27.5±3.1	22.6±5.2	14.6±3.1
4. 'Eyrean'	17.4±1.6	6.9±1.7	30.6±2.6	23.8±3.3	13.3±3.2	21.6±3.6
5. 'Eyrean'	15.3±1.9	4.6±2.0	28.4±2.6	23.6±3.5	12.3±4.0	18.9±3.9
6. 'Bassian'	15.2±4.2	4.5±3.8	26.1±3.2	16.0±5.2	15.7±7.2	15.3±3.8
7. 'Bassian'	14.8±2.0	3.6±2.6	25.5±1.2	22.0±1.7	18.5±1.9	11.6±3.3
8. 'Bassian'	18.1±2.7	6.0±3.3	28.4±2.4	22.4±3.3	21.5±4.1	15.0±3.1
9. 'Torresian'	24.8±2.6	14.4±3.8	33.1±2.6	18.7±3.7	27.0±1.8	21.9±3.2
10. 'Torresian'	25.9±1.9	16.1±3.4	33.9±3.4	18.0±4.0	27.7±1.4	23.4±2.3

(B) Precipitation based indices (units mm)

	Annual mean precipitation	Precipitation wettest month	Precipitation driest month	Annual precipitation range	Mean precipitation wettest quarter	Mean precipitation driest quarter
1. 'Eyrean'	617±432	109±91	17±18	92±91	326±254	61±60
2. 'Eyrean'	340±120	64±29	8±8	55±31	168±75	31±26
3. 'Eyrean'	675±192	95±40	32±8	66±41	260±106	106±25
4. 'Eyrean'	671±351	132±70	10±5	121±70	351±183	39±16
5. 'Eyrean'	423±204	51±23	21±14	31±17	145±67	70±44
6. 'Bassian'	1074±438	146±87	47±19	99±85	410±237	152±44
7. 'Bassian'	1146±206	130±30	62±9	68±24	365±82	205±30
8. 'Bassian'	1193±466	176±103	47±16	129±89	490±279	162±55
9. 'Torresian'	1395±530	314±114	16±19	303±110	861±313	57±65
10. 'Torresian'	1341±340	319±83	7±10	312±81	875±232	28±32

The fifth group comprises only three species, *Drysdalia mastersii* (Map 23), *Unechis spectabilis* (Map 76) and *Unechis flagellum* (Map 71) and their core distribution also lies within the winter wet/summer dry zone, but has a significant eastward shift when compared with the previous group. *Unechis flagellum* is confined to the southeast, but both *Drysdalia mastersii* and *Unechis spectabilis* extend westwards around the Great Australian Bight to the vicinity of Esperance.

In bioclimatic terms then the elapid snakes of southwestern Western Australia have closer affinities with the arid and continent-wide Eyrean group than with those of the Bassian zone. Only one Bassian zone species (perhaps more following taxonomic revision of the complex!), *Notechis ater,* occurs in the southwest of Western Australia.

The basically mesotherm mesic Bassian zone is divided into three bioclimatic sub-regions and these

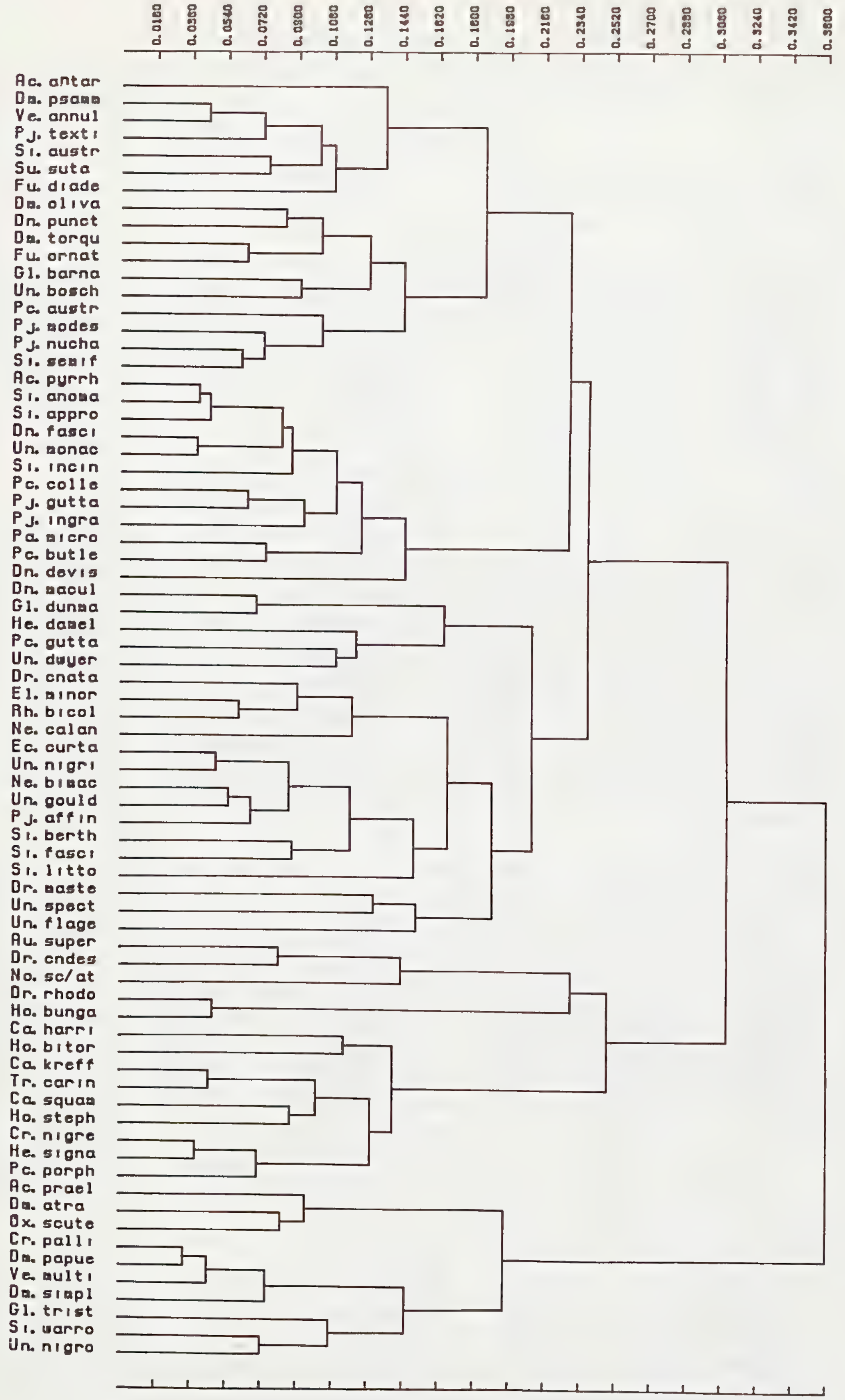
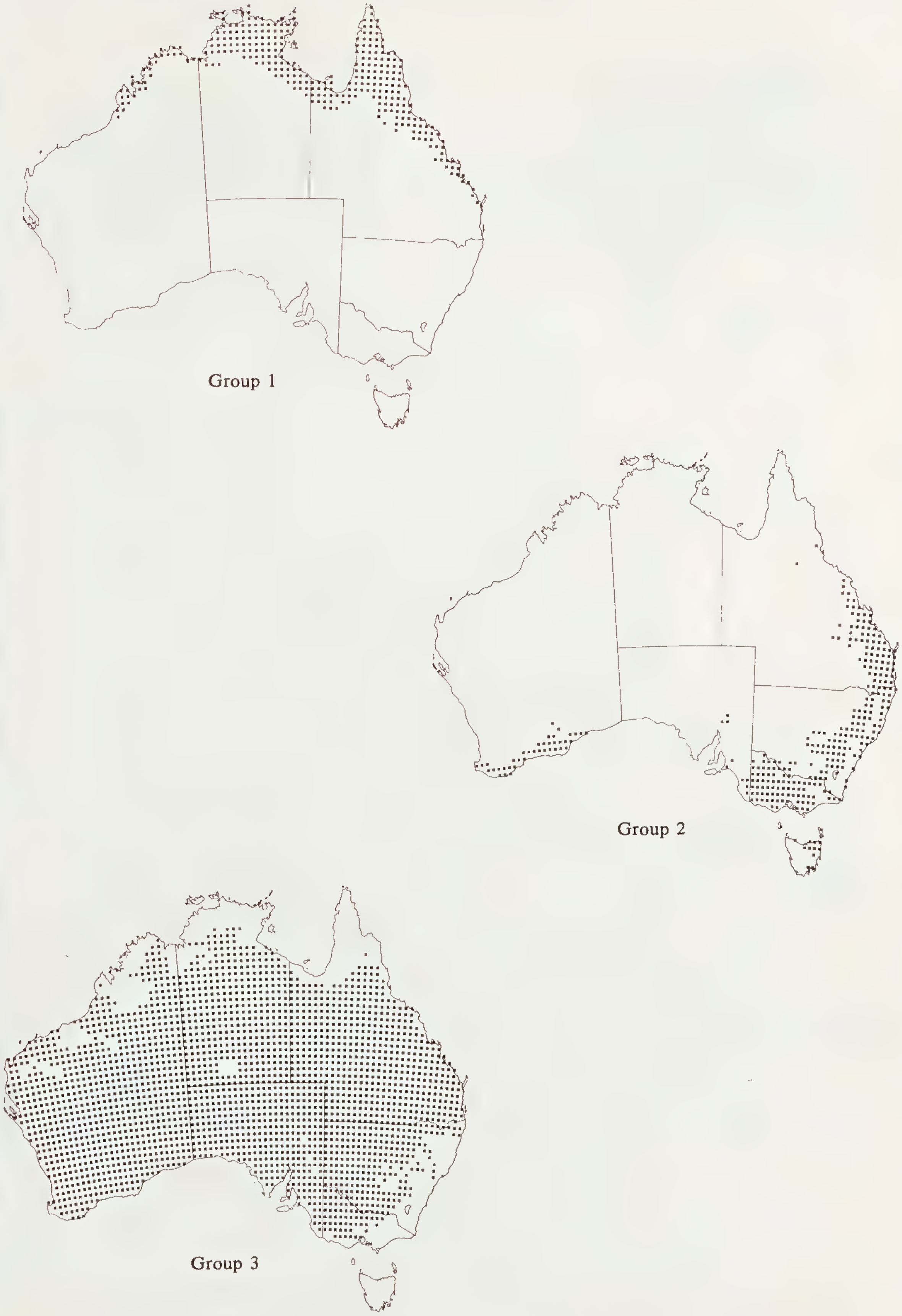


Figure 1. Dendrogram showing relationships of 73 elapid snake taxa in terms of similarity of their bioclimatic profiles, using the Numerical Taxonomy Package (NTP) with ASO (Gower metric) and FUSE (UPGMA strategy)

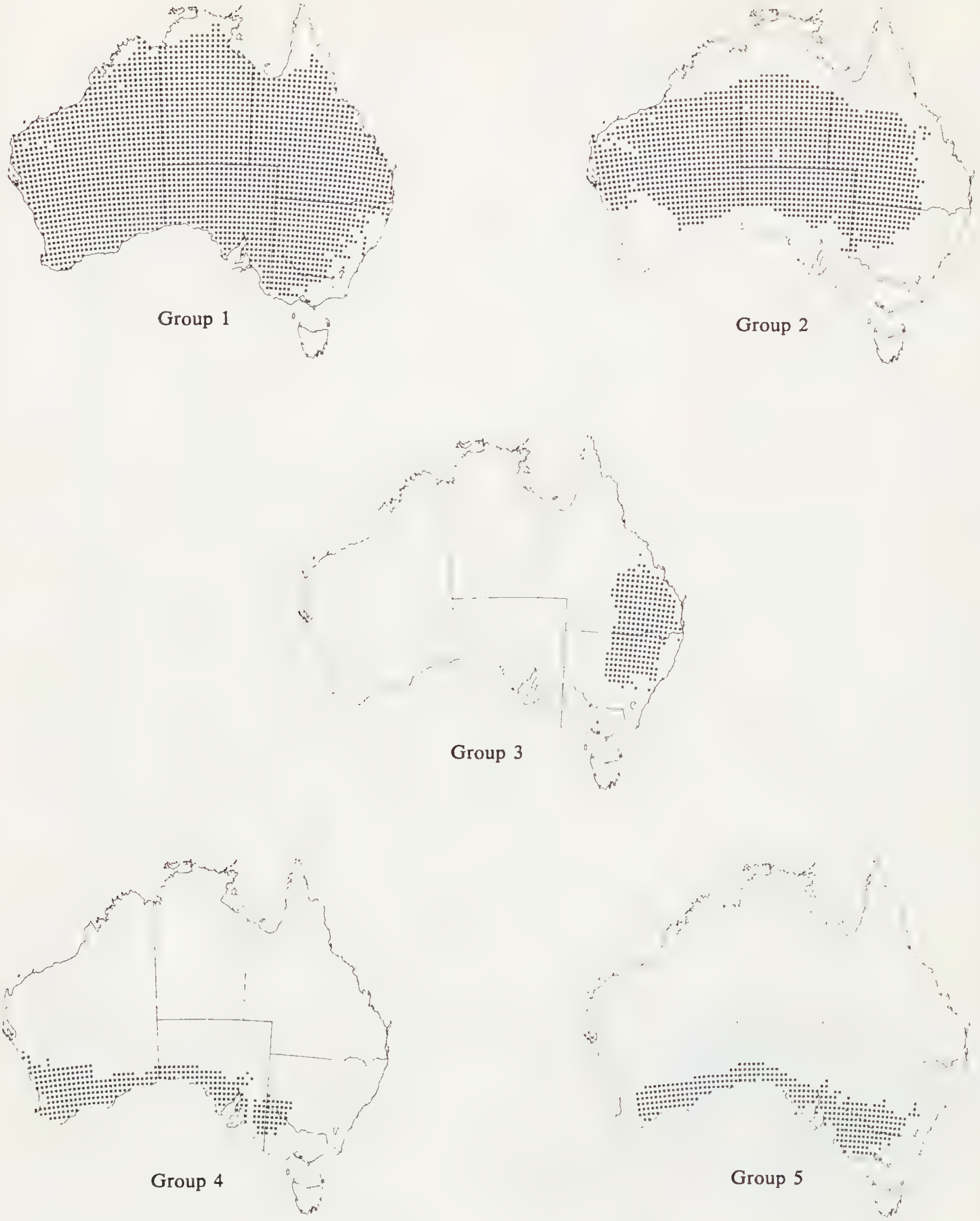


Group 1

Group 2

Group 3

Figure 2. Zoogeographic regions of Australia at 3 group level based on classification of bioclimatic profiles of component elapid snake taxa, recalculation of new profiles for each group and plotting core distribution by 0.5° grid



Group 1

Group 2

Group 3

Group 4

Group 5

Figure 3. Zoogeographic regions of Australia at 10 group level based on classification of bioclimatic profiles of component elapid snake taxa, recalculation of new profiles for each group and plotting core distribution by 0.5° grid

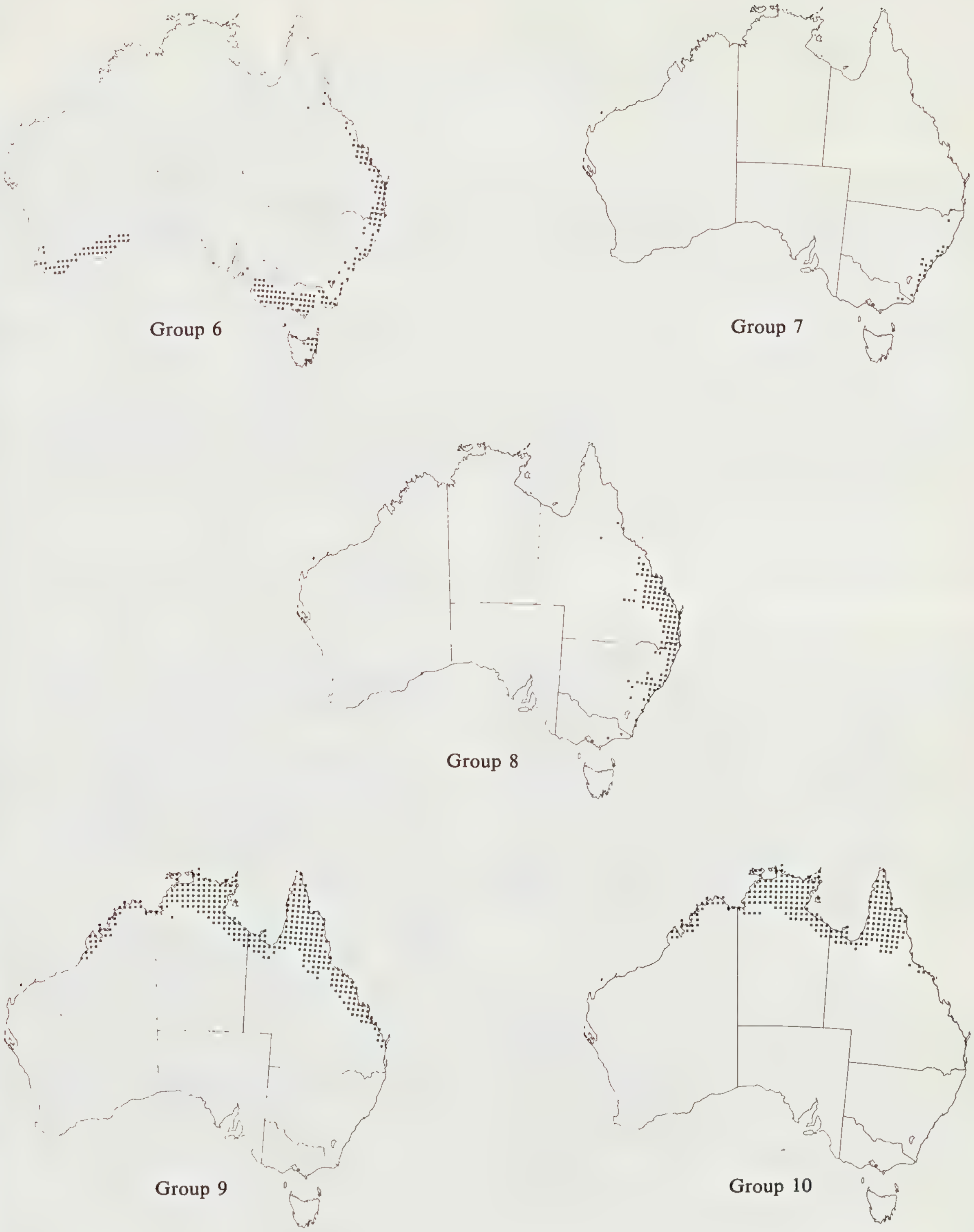


Figure 3. (cont.) Zoogeographic regions of Australia at 10 group level based on classification of bioclimatic profiles of component elapid snake taxa, recalculation of new profiles for each group and plotting core distribution by 0.5° grid

are groups six, seven and eight of the ten group classification. The sixth group comprises only three species. *Austrelaps superbus* (Map 4) and *Drysdalia coronoides* (Map 22) are distributed widely in southeastern mainland Australia and Tasmania while the *Notechis* spp. complex (Map 42) extends this distribution around the southern coastline and into the southwest of Western Australia.

The seventh group comprises only two species and *Drysdalia rhodogaster* (Map 24) and *Hoplocephalus bungaroides* (Map 36) have their core distribution within central eastern N.S.W. The eighth group comprises nine species with an east coast distribution and with outliers inland and further north on cooler, moister tablelands and mountains. Several species appear to be centred in southeastern Queensland and northern N.S.W., but with outlying populations in far north Queensland, see *Cacophis harriettae* (Map 5), *Hoplocephalus bitorquatus* (Map 35), *Tropidechis carinatus* (Map 68), *Cacophis krefftii* (Map 6) and *Cacophis squamulosus* (Map 37). *Hoplocephalus stephensii* (Map 37) has the same basic pattern, but does not appear to extend to far north Queensland. Three species, *Cryptophis nigrescens* (Map 8), *Hemiaspis signata* (Map 34) and *Pseudechis porphyriacus* (Map 49), have even wider distributions extending southwards and inland.

The basically megatherm mesic Torresian zone is divided into two bioclimatic components and these are groups nine and ten in the classification. Although the maps of core distributions for these two groups appear very similar (Figure 3), as do the means and standard errors for the twelve bioclimatic indices (Table 2), there are significant differences between them. Group nine comprises three species, *Acanthophis praelongus* (Map 2), *Demansia atra* (Map 10) and *Oxyuranus scutellatus* (Map 43), which range across the whole of northern Australia and most significantly, into the very high rainfall zones of northeastern and eastern Queensland. All three species also occur in New Guinea.

Group ten comprises seven species with a core distribution that is characterised by very high precipitation seasonality *i.e.* the so called monsoonal climate zone with wet summers and extremely dry winter and spring months. Thus, a specimen-based estimate of the mean precipitation of the driest quarter for this group is 28 mm. This value is comparable (32 mm) with that for the driest quarter in the arid zone group (group two). Also, the upper limit to annual mean precipitation for this group at 1564 to 2400 mm is significantly lower than that for the previous group at 3553 to 4027 mm. Four of the species in this group, *Cryptophis pallidiceps* (Map 9), *Demansia papuensis* (Map 12), *D. simplex* (Map 14) and *Vermicella multifasciata* (Map 78), are known only from the 'Top End' of the Northern Territory and the Kimberley region, although suitable bioclimate matches occur at the base of the Gulf of Carpentaria and southwestern Cape York Peninsula. Extensive areas of cracking clay plains at the head of the Gulf of Carpentaria possibly have acted as a barrier. The remaining three species, *Glyphodon tristis* (Map 32), *Simoselaps warro* (Map 66) and *Unechis nigrostriatus* (Map 75), occur in Cape York with extensions southward into seasonally dry environments along the northeast coast *e.g.* Townsville-Bowen and Rockhampton-Gladstone for *U. nigrostriatus*.

DISCUSSION

The biogeographical analysis presented here differs from all others that have preceded it. The methods used are explicit, quantitative and specimen based. Previous methods have relied on presumed presence/absence data using generalised distribution maps and a point or grid sampling procedure. This method builds up a quantitative description of environment (bioclimatic profile) from point data for each taxon, groups taxa with similar profiles, recalculates new group profiles and then plots distribution patterns based on these shared requirements. Even so there are problems and limitations with this new procedure.

In any classification, the choice of attributes, the method of scaling or measurement, the type of association measure used and the classificatory strategy used can materially influence the end result. Possibly, for instance, use of indices derived from a water-balance model that took account of precipitation, evaporation and soil water storage, rather than those derived from precipitation alone would have altered groupings. Because in general precipitation declines and evaporation increases inland the effect would be to heighten differences between more coastal and inland distributions. In such a case, some of the taxa now placed with the continent-wide 'Eyrean' zone possibly would be reallocated to the 'Bassian' or 'Torresian' zones.

Examination of the bioclimatic profile data in Tables 1 and 2 emphasises the importance of temperature for reptiles. The continent-wide Eyrean and northern Torresian zones contain 59 of the 73 species. Thus, slightly more than 80% of elapid snakes analysed occur only in areas where annual mean air temperature exceeds 14°C.

Differences in the water regime are not well indicated by precipitation indices as pointed out earlier. The apparently unusual continent-wide Eyrean distribution may be explained by an intolerance of regular seasonal soil saturation by some of these basically terrestrial species. Certainly the isoline for mean duration of soil profile saturation equalling or exceeding three months closely parallels the outer boundary of this group. That this pattern has some reality is confirmed by the significant number of so-called 'Eyrean' species of other vertebrate groups *e.g.* birds, mammals, amphibians that closely approach the eastern and southern coastline at a number of points.

Until problems of higher level taxonomy are resolved there is little to be gained in discussion of the possible relevance of the patterns generated for elapid evolution on the Australian continent. What would be possible, however, would be to postulate past climates, modify the grid and generate predicted distributions of species groups according to these climates. Of course, the limitation here is our current inability to make more than the crudest estimates of annual temperature and precipitation changes for past climates.

Of the currently recognised genera, nine occur in the Bassian zone (*Austrelaps, Drysdalia, Notechis, Hoplocephalus, Cacophis, Tropidechis, Cryptophis,* *Hemiaspis* and *Pseudechis*) with only one genus (*Cryptophis*) shared with the Torresian zone and three genera (*Drysdalia, Hemiaspis, Pseudechis*) with the Eyrean zone. The Torresian zone has eight genera, one of which (*Cryptophis*) is shared with the Bassian zone, while seven are shared with the Eyrean zone (*Acanthophis, Demansia, Parademansia = Oxyuranus, Vermicella, Glyphodon, Simoselaps* and *Unechis*). The Eyrean zone, as here defined, has eighteen genera, with three genera shared with the Bassian zone and seven genera shared with the Torresian zone. This leaves eight genera that are confined to the Eyrean zone (*Pseudonaja, Denisonia, Suta, Furina, Elapognathus, Rhinoplocephalus, Neelaps, Echiopsis*).

Although bioclimate has been useful in beginning to define the environmental domains of elapid snakes, obviously other factors play an important role in the realised niche of a given taxon. Substrate must be particularly important, with soil texture, surface soil albedo, presence/absence of deep cracks, stoniness, depth of litter, presence/absence of fallen dead timber, termite mounds, animal burrows and surface water all being important. Factors that influence distribution and abundance of prey and predator species likewise are of importance. In time, and with more systematic observation and more comprehensive records, we may develop more appropriate procedures for definition and delineation of environmental domains.

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COMMENTS ON THE BIOGEOGRAPHY OF THE ELAPID SNAKES OF SOUTHEASTERN AUSTRALIA

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Distribution patterns of animals and plants are dynamic. Their boundaries change constantly as a result of local, regional or global environmental changes, or of changes in the population genetics of species. For example, the clearing of forest for agriculture today will bring about a change in the distributions of many of the animals and plants which originally inhabited that forest. Similarly, the introduction of the rabbit to Australia by Europeans in the late 18th century or the advancing glaciers of the great Ice Ages of the Pleistocene Period have had profound effects on the distribution of the animals and plants then inhabiting Australia.

The primary tasks of the biogeographer are to document the present distribution of animals and plants and to attempt to identify the historical and contemporary facts which have led to the patterns which we observe today. With this information the biogeographer then is able to attempt two kinds of predictions:

1. Where and under what conditions animals and plants should be found (even though we may not yet have found them there)?
2. What would be the effects on the distribution of particular animals or plants of specific changes to the climatic, physical, chemical and biological environments in which they live?

This process usually begins with a map. The more accurate and complete the map and the more detailed the records on which the map is based, then the greater is its predictive quality.

Australia has a unique complement of venomous snakes making up nearly 70% of its large land snake fauna. These snakes, traditionally assigned to the cobra family (Elapidae), include the most deadly snakes in the world and so are of very considerable interest to Australians who have to share their country with them. And because some 75% of Austalia's 15 million people live in southeastern Austalia, it is of no small consequence that the maps in this *Atlas* provide us with the most up-to-date information on the occurrence of venomous snakes in this region. Such information has a multiplicity of uses, from identifying key locations for maintaining stocks of anti-serum to the recognition of areas of outstanding conservation value.

In order to interpret the patterns of distribution revealed in the maps, it is important to have some understanding of the principal topographic and ecological features of southeastern Australia (including those which have been dramatically altered by man during the past two centuries) and of the history of climatic changes in the region.

The dominating physiographic feature is the Great Dividing Range, which reaches its greatest altitude in the southeast (2228 metres). Rising only a short distance from the coast and running more or less parallel to it for most of its length, the Great Divide captures the moisture-laden clouds from the eastern seaboard. That moisture is returned to the sea via a series of short, flood-prone rivers flowing through a narrow, well-watered and forested coastal zone which has been subjected to intensive clearing for farming, timber or urbanisation. The ranges and their steep eastern escarpments have been exploited less by man and retain a much greater proportion of their original vegetation, including a series of isolated patches of sub-tropical rainforest in the north. These patches extended to the coast in many places when Europeans first arrived, but the lowland stands were soon cleared. In the southwest of southeastern Australia the Great Dividing Range breaks up into a series of outlying ranges, isolated from the semi-arid Mt Lofty and Flinders Ranges in South Australia by an extensive flatland through which runs the Murray River.

West of the Great Dividing Range the country rapidly becomes drier. The western slopes are characterised by dry, open woodlands which gradually merge with the mosaic of shrublands and grasslands of the western plains. Through these plains pass a series of meandering, slow-flowing rivers which, when in occasional flood, spread out over vast areas of adjacent flood-plain. In the far west of the region, a series of salt-lakes, gibber plains and dune fields are the eastern outliers of the arid and desert interior of Australia.

Off the southeastern coast of the continent and isolated from it by the cold and turbulent waters of Bass Strait, lies Tasmania. A complex of temperate wet forests, woodlands and grasslands, Tasmania has an impoverished reptile fauna, in part reflecting its cool temperate climate.

Historically, the snakes of southeastern Australia have been seen to fit into a broad pattern of biogeographic subregions first characterised in the late 19th century by Tate (1887), Hedley (1893,1895), Hutton (1896) and Spencer (1896). These workers recognised a number of major faunal regions in Australia, to which they gave a variety of names. The simplest classification was that of Tate (1887) who recognised three faunal divisions - an ancient assemblage which developed "in place" in Western Australia and which he called the *Autochthonian*, another assemblage, the *Euronotian*, which developed in the east from a fauna derived from South America via Antarctica and a desert-adapted mixture of these two which he called the *Eremian*. Hedley and Spencer both recognised, in addition, a strong tropical element which they believed had originated to the north of Australia and which they called the *Papuan* or *Torresian*. However it was Spencer (1896) who set the scene for most of the 20th century with his three faunal subregions: a northern Torresian, an arid Eyrean and a southern Bassian. Although this pattern has been discussed and refined by many subsequent workers (see Keast *et al.* 1959; Keast, 1981) and has widely been regarded as applying to reptiles in general, only recently have biologists come to accept that even *within* each group of animals the adaptive radiations which we observe today have resulted from very different chronologies and thus very different conditions. Cogger & Heatwole (1981) showed that the patterns of species density and geographic relationships in elapid snakes were very different from those of a number of other families of Australian reptiles. Appendix 2 shows that there are regional pockets of *predicted high species diversity* (25 or more species) only in southwestern Western Australia, southeastern South Australia and eastern Queensland with, surprisingly, the highest density of all occurring in central eastern Queensland. These densities are greater than, but closely parallel, those based on known distributions in Cogger & Heatwole (1981 p. 1366).

The significance of such centres of high species diversity is uncertain. They are sometimes thought to represent "dispersal centres" or "centres or origin". Dispersal centres are areas to which ancestral populations retreated and survived when climatic and other changes reduced the geographic range of viable habitats available to particular species or populations. Later, when conditions ameliorated and the habitats spread out into all or part of their former ranges, so too did many of the animals which inhabited them. Centres of origin, on the other hand, represent areas in which particular adaptive radiations have been focused. One view of such centres is that they represent areas in which advanced forms predominate as the result of the gradual outward displacement of primitive forms. An opposing view is that primitive forms predominate in these centres as a result of the greater vagility or adaptability of advanced forms which allows them to exploit new or marginal environments. Both of these views are testable only when the phylogeny of a particular group and hence the phylogenetic polarity of particular species, is known. The phylogeny of Australian elapids is still too poorly understood to apply these tests.

Except for the centres of high species diversity cited above, throughout the remainder of the continent, whether wet or dry, coast or interior, tropical or temperate, the number of elapid snakes in any given area averages only about 10 species. Only in southern Victoria and Tasmania does the number of species decrease significantly.

This pattern is reflected in the distribution maps of this *Atlas*. There is no one region in southeastern Australia in which elapid snakes are especially diverse; rather, the number of species is lowest in the colder regions of Tasmania and the southern alps and is highest where topographic and habitat diversity is greatest (southeastern South Australia and the border region between northeastern New South Wales and southeastern Queensland).

While many early Australian biogeographers, on the basis of observed faunal relationships, considered that much of the continent's biota was derived from an earlier southern continental land mass connecting Australia to South America, only recently has geomagnetic data confirmed that Australia was part of a giant southern continent (Gondwanaland) which comprised what are now Australia, New Zealand, Antarctica, South America, India and Africa and which commenced to break up about 200 million years ago. Australia parted from the remains of this super-continent about 60 million years ago, slowly drifting northwards from Antarctica to its present position.

Were there snakes present in Australia at that time? Certainly there is no evidence that there were, although Hedley (1895) considered that most of our present snake fauna is derived from a Gondwana relict. Current opinion gives a much later origin for our snakes, including elapids (Cogger & Heatwole, 1981), presumes that ancestral forms arrived from Asia and that the relative isolation of Australia provided the opportunity for a massive adaptive radiation *in situ*.

Because there is virtually no fossil record of elapid snakes in Australia beyond the Pleistocene, the chronology and origins of the Australian radiation remains conjectural. While Storr (1964) considered that elapid snakes constituted "one of the oldest elements in the Australian herpetofauna", recent studes of their cytology and genetics indicate that Australian elapid snakes are not only far removed from their relatives in other parts of the world, but that today's elapid fauna is the result of a quite recent radiation, perhaps no older than 12 million years, and separation from the Asian elapid stock dates back to about 20 million years (Schwaner *et al.*, 1985). These data indicate either that our present elapid snakes evolved from a more ancient fauna that already existed in Australia and Asia, but whose nature and origin remain obscure, or that their ancestors reached Australia from Asia, after which the two areas were effectively isolated so that their respective snake faunas radiated independently. There is difficulty accepting this latter scenario given that Australia, 20 million years ago, was much further removed from Asia than at any time since.

If Australia's elapid radiation is only 10–15 million years old, under what kinds of conditions did it evolve? By middle Miocene times, about 15 million years ago, Australia had drifted considerably north of Antarctica but still well south of its present latitudes. Having recently undergone a period of great aridity, its climate was by this time much more equable. The seas were warm and what is now the arid interior was probably wooded, with large lakes (Quilty, 1984). Australia at this time, however, appears to have been cut off from direct contact with other faunas, having severed its links with Antarctica but only just beginning to collide with the Asian plate. By the late Miocene, about seven million years ago, Australia had more or less taken on its present topography and shape. It was connected to New Guinea and Tasmania and its contact with southeast Asia provided opportunities for animals and plants of that region to migrate to Australia. Conditions generally became cooler and drier. During the Pleistocene Epoch of the past 1.8 million years, Australia passed through a number of periods of warm, dry conditions alternating with periods of moist, cool conditions. A series of perhaps 20 or more Ice Ages at times resulted in changes in sea levels of more than 100 metres and extensive land bridges were formed and broken between continental Australia, New Guinea and Tasmania. The present seawater straits between continental Australia, New Guinea and Tasmania were land bridges as recently as 12000 years ago. Aridity leading to the formation of the distinctive dunefields of central Australia probably began about 35 million years ago, but the dunefields themselves are probably less than five million years old (Williams, 1984). At various times the area which is now represented by the arid Nullarbor Plain, was moist and wooded and provided opportunities for mesic-adapted species, such as Tiger Snakes *Notechis* spp. to range more or less continuously between east and west.

What, then, are the major biogeographic features which today characterise the elapid snake fauna of southeastern Australia? Collectively, the number of species decreases markedly with increasing latitude. Some 16–20 species occurring in the northeastern corner of this region reduces to half that number in southern Victoria and this figure is halved again in Tasmania. This rich northeastern component represents a southern extension of a tropical fauna which extends into southeastern Australia via the rainforests and associated wet sclerophyll forests of the coast and adjacent ranges and is typified by such species as the Rough-scaled Snake *Tropidechis carinatus* (Map 68), Stephen's Banded Snake *Hoplocephalus stephensii* (Map 37) and the little crowned snakes of the genus *Cacophis* (Maps 5–7).

The upland areas of the Great Dividing Range have provided a corridor via which species adapted to cool temperate conditions have been able to extend northward into the otherwise subtropical parts of this region. Or perhaps, as seems more likely, these species were more widely distributed northward during the last glaciation in southeastern Australia and their present northern montane populations are relicts from that former distribution. Obvious examples are the Copperhead *Austrelaps superbus* (Map 4), Mainland Tiger Snake *Notechis scutatus* (Map 41) and White-lipped Snake *Drysdalia coronoides* (Map 22).

West of the Great Dividing Range a tropical or northern element is represented by a distinctive assemblage of species found in the woodlands of the northwest slopes and the adjacent well-watered plains. The Spotted Black Snake *Pseudechis guttatus* (Map 48), Devis' Banded Snake *Denisonia devisi* (Map 16) and the Grey Snake *Hemiaspis damelii* (Map 33) fall into this category. Some members of this group have been able to breach the Dividing Range and reach the east coast by following the relatively low, dry corridor at the headwaters of the Goulburn and Cudgegong Rivers into the Hunter Valley. Conversely some essentially mesic species, such as the Red-bellied Black Snake *Pseudechis porphyriacus* (Map 49) have extended their ranges well into the dry interior by exploiting the narrow mesic corridors represented by the riparian systems of the Macquarie, Lachlan and Darling Rivers.

In the west of the region under discussion, arid-adapted forms predominate and generally represent either the eastern boundary of the centralian desert fauna (for example, the Narrow-banded Snake *Simoselaps fasciolatus* (Map 61) and the Ringed Brown Snake *Pseudonaja modesta* (Map 53) or an eastern extension of a semi-arid fauna associated with open-scrub and low shrubland, as exemplified in the mallees and chenopod scrubs of western Victoria and southwestern New South Wales. The Bardick *Echiopsis curta* (Map 26) and Master's Snake *Drysdalia mastersii* (Map 23) are representatives from this latter group.

None of the elapid snakes found in Tasmania are confined to that island and they represent no more than an outlier of the Victorian fauna. Sea level fluctuations during the Pleistocene, however, resulting in episodic island formation in Bass Strait and along the continental shelf of southern Australia, appear to have led to the recent evolution of distinctive morphological, biological and ecological characteristics in many of the island and mainland populations of tiger snakes (currently assigned to only two species, *Notechis scutatus* and *Notechis ater* Map 40). The effects of the more recent Quaternary glaciations in southeastern Australia, especially as they relate to the Tasmanian reptile fauna, have been discussed at length by Rawlinson (1974). Of the three elapid species which occur in Tasmania (the Copperhead, *Austrelaps superbus*, the White-lipped Snake, *Drysdalia coronoides*, the Black Tiger Snake, *Notechis ater*), Rawlinson regarded all three as glacial relicts, *i.e.* their Tasmanian populations are relicts, isolated by the last flooding of Bass Strait, of species which were widespread in southeastern Australia during the late Wisconsin glacial phase (approximately 15000–30000 years ago).

It is evident from the maps that the taxonomic relationships of the various populations of tiger snakes *Notechis* are far from clear, and Schwaner (1985) has shown that the ecology and morphology of tiger snake populations from isolated but geographically proximate islands vary greatly, despite almost certain close genetic affinity. He attributed these differences to the adaptive effects of different food resources on the different islands. Schwaner also considered *Notechis scutatus* and *Notechis ater* to be members of the same species complex. Consequently Rawlinson's (1974) suggestion that the Mainland Tiger Snake *Notechis scutatus* is a post-glacial intrusive (*i.e.* it invaded the southeast of the continent less than 10000 years ago) is difficult to sustain.

It will be obvious from the maps that there are many species which do not fit comfortably into any of the groupings listed above. Most of these species, such as the brown snakes *Pseudonaja* spp. (Maps 50–55), the Death Adders *Acanthophis* spp. (Maps 1–3), the Mulga Snake *Pseudechis australis* (Map 45), the Bandy Bandy *Vermicella annulata* (Map 77) and the Yellow-faced Whip Snake *Demansia psammophis* (Map 13) occupy a diverse array of habitats from coastal forests to arid scrublands and their ranges extend well beyond southeastern Australia. These ecologically vagile species are difficult to categorise; a number may prove to consist of a complex of species each of which has a more discrete range which would bring it into one of the groups described above. The maps themselves, with their BIOCLIM profiles, will greatly assist the taxonomist in sorting out such species complexes.

Of course, distribution maps are made by humans and so not only reflect the distribution of the species being mapped but also the distribution of human populations and their activity patterns. This is clearly evident in the maps of this *Atlas*, where actual records tend to be clustered around centres of population or along roads and tracks. Nevertheless, because of a multiplicity of factors (the distribution of past and present climates and habitats, topographic features, habitat changes wrought by man and the biological and ecological characteristics of particular species - all interacting to produce the distributions shown in the maps), the observed distribution patterns tell us a great deal about each of these factors. For example, Shine & Berry (1978) showed that there is a strong correlation between mode of reproduction and latitude: egg-laying species predominate in the north of Australia and live-bearing species predominate in the south. Schwaner *et al.* (1985) have indicated that the radiation of viviparous elapids is an extremely recent (Quaternary) event and Shine (1985) has correlated this radiation with the advent of cooler continental conditions during this period.

Whereas the ecologist is primarily concerned with the manner in which a species is distributed *through* its range, the biogeographer is more concerned with the factors which determine the *geographic limits* of that range. Thus by correlating overall distributions with a number of important environmental variables this *Atlas* will provide both the ecologist and the biogeographer with a unique foundation on which to erect a new and more complete understanding of the origins of the elapid snake fauna of Australia and of the factors which have brought about and govern its present distribution.

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ASPECTS OF THE BIOGEOGRAPHY OF THE ELAPID SNAKES OF NORTHEASTERN AUSTRALIA

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"... it is curious how interesting it can be to talk about things we supposedly can't talk about..." Rudy Rucker

"To understand why a particular group of organisms is found in a specific area requires knowledge of the organism's ecological relationships - why it is associated with this soil, this temperature range, or this type of woodland. To understand why it is found in particular areas of a continent may require knowledge of the climatic history, which may have led to the isolation of scattered relict communities. Finally, to understand why it is found in some continents and not in others involves knowledge of the evolutionary history of the group itself and of the geological histories of the land masses" (Cox & Moore, 1980).

In attempting to explain the occurrence and patterns of distribution of the elapid snakes of northeastern Australia it quickly becomes apparent that, while a good deal is known about *where* they occur, there is a dearth of information on which to base explanations about *why* they occur where they do. The maps presented here summarise for the first time elapid distribution data acquired over the last 100 years or so. The geological and climatic history of this continent is well documented (e.g. Frakes & Rich, 1982 and references therein), but the fossil record for elapids is almost non-existent and phylogenetic work on them is in its infancy.

"Australia and its biotic composition have not only been affected by changing associations with other continents, by severe isolation and changing world climates, but have also been affected by changing latitude ... Australia was in an equatorial position and rotated 90° to its present orientation during the Ordovician, when the first vertebrates occur on this continent. Subsequently, in the Silurian and Devonian, it moved south into higher but still subtropical and temperate latitudes and rotated more towards its present day orientation. By the Carboniferous and Permian, it had moved decidedly further south into temperate and even polar latitudes. During the Mesozoic, Australia remained in much the same southerly position, even when New Zealand broke away in the late Mesozoic, and it wasn't until the Eocene that once again the continent changed latitudes, moving northwards to near its current position by the Miocene, after crossing several degrees of latitude" (Frakes & Rich, 1982).

It is apparent that the Australian biota is a complex mix from an early Gondwanan primary element and a more recent Laurasian element. Both elements, of course, have also evolved significantly since reaching Australia. Minton (1981) notes "Australian elapids may have evolved *in situ* or arrived early from some other Gondwanaland region. They evidently arrived in the Australian continent ahead of the colubrids".

There is virtually no Australian fossil record for the elapids (nor for many of the other extant families of reptiles *e.g.* gekkonids, typhlophids; Molnar, 1982, 1985). The oldest known fossil snakes in Australia are boids from the Miocene (*c.* 15 m years ago). Most of the few fossil elapids known are from the Pleistocene (1 m to 10,000 yrs before present) from one site, Naracoorte, S.A. These included forty unidentified vertebrae and some skull remains referred to genera of living forms - *Notechis, Pseudechis* and *Pseudonaja* (Smith, 1976). Other snake fossils are known from the Pliocene (4.5 m yrs) Allingham formation, NE Qld. Included is one vertebra of a possible elapid (Archer & Wade, 1976). All that can be said with certainty about the origin of elapids in Australia is that representatives of three of the extant genera of large elapids have occurred here for close to 1 m years. Naracoorte is a coastal locality where species of all three genera still occur. Such scant fossil evidence contributes nothing to either an understanding of the ancestry of the elapids or to understanding why the "elapid radiation has produced a large number of species with considerable morphological diversity" (Minton, 1981).

Mengden (1983) and Cogger (1985) have reviewed current classification of Australian elapids. Work to produce a widely accepted (or, at least, tolerated) classification which reflects phylogenetic relationships has really only just begun, with studies by Baverstock & Schwaner (1985), McDowell (1985), Mengden (1985a,b), Schwaner *et al.* (1985), Shine (1985), Storr (1985) and Wallach (1985). No reviews based on cranial comparisons between many genera have been completed although McDowell (1967, 1968, 1969a,b, 1970, 1972, 1974) has discussed relationships between Australia's elapids and hydrophiids at length, and one generic rearrangement (for *Oxyuranus*) based on external and cranial morphology, venom, cranial musculature, morphology of the hemipenis, behaviour and karyotypes has been completed (Covacevich, *et al.* 1981). Smith *et al.* (1977), following McDowell's work, suggested that Australia's elapids should be treated more properly as hydrophiids. This placement reflects McDowell's conviction that the affinities of Australia's elapids lie with the sea-snakes (Family Hydrophiidae) rather than with elapids of Africa and Asia. This 'new' family allocation has not gained wide acceptance and is used only infrequently. Below the family level, species are well known and definitions are fairly stable, but many generic allocations appear to be based on convenience, tradition and whim rather than a synthesis of morphological (especially cranial), biochemical and cytological data - a basic prerequisite to understanding relationships.

It seems reasonable then, not to try to proceed with a complete zoogeographic treatment of the elapids. With such incomplete data it seems best to focus on their distribution patterns - the *wheres* about taxa occurring in the north and east of the continent. It is wise to remember that it is barely 20 years since the present position of the continents was the basis of all zoogeographic interpretations. Further, it must now be recognised that concepts in Australasian zoogeography have changed greatly since an ancient Gondwanan origin of much of the flora/fauna of the region has gained wide acceptance. "Whether the Australo-Papuan genera ... (of elapids) are the lone survivors from a formerly widespread group or are locally derived from one or two immigrants is unknown; but in either event they must constitute one of the oldest elements, in the Australian herpetofauna ...". This statement (Storr, 1964) prior to wide interest in and acceptance of the concept of Gondwanaland and moving continents, contrasts sharply with current views (based on immunological studies) that Australia's elapids have very recent (Pliocene, 5–1 m yrs) origins (Schwaner, pers. comm.).

Forty-eight species of elapids currently assigned to 18 genera occur in northeastern Australia - broadly the eastern Northern Territory and Queensland. It can be inferred from present distribution patterns that elapid genera presently occurring in northeastern Australia have originated primarily in the north and east of the continent (Table 1).

To pursue this hypothesis, it is necessary to make some assumptions.

1. Present distribution patterns *can* be useful in pointing to origins (this flouts the advice of Bishop (1981) who warns against "drawing facile conclusions from recent distributions").
2. The occurrence of a high proportion of species of a genus in an area may point to its being a centre of diversity for that genus.
3. Large scale extinctions of species of elapids since the Pliocene (approximately 5 m yrs) would be unlikely.

In the absence of contrary (in fact, *any*) fossil evidence, the proposal that elapids of the northeast have recent, essentially *in situ*, origin seems worthy of investigation.

All 'northern' Australian genera and many of their species also occur in New Guinea - *Acanthophis antarcticus* (? *A. praelongus/A. laevis* of Cape York and southern New Guinea), *Demansia olivacea, D. papuensis* (the status of this species on Cape York Peninsula has yet to be determined), *Demansia psammophis, Glyphodon tristis, Oxyuranus scutellatus.* In addition, species from genera regarded as 'eastern' and 'western' have also crossed to (or from) New Guinea - *Pseudechis australis, Unechis boschmai, Unechis nigrostriatus.* What might be termed 'the New Guinea connection' between plants and animals of northern Australia is both well known and well documented for the reptiles. New Guinean and Australian reptile associations have been discussed by Storr (1964), Tyler (1972), Covacevich & Ingram (1980), Kikkawa *et al.* (1981) and Covacevich & McDonald (1984). Most Australian species of elapids which also occur in New Guinea are grassland and open-forest inhabitants, as are most of the frogs and other reptiles common to both regions. The high number of open-forest species (*vs* the few rainforest species) shared between the two areas can be explained in the light of recently published data on the Quaternary 'scene' in the north (Bowler *et al.* 1976; Chappell, 1976; Kershaw, 1975; Galloway & Kemp, 1981). During the last 120 000 years there have been extensive land bridges between New Guinea and Australia and low precipitation (with consequent reduction and fragmentation of rainforests). These conditions have provided ample opportunity for colonisation north to, and south from, New Guinea for inhabitants of grasslands and open-forests. *Acanthophis,* in New Guinea, is supremely indifferent to habitat. It is found from open grasslands of the south coast and central highlands, rainforest throughout its range and limestone outcrops up to nearly 2000 m in the central highlands (F. Parker, pers. comm.). Successful migration of rainforest reptiles has been relatively infrequent, a result, no doubt, of successive expansions and contractions of rainforests with alternating relatively wet and dry conditions.

TABLE 1 Centres of diversity (? possibly indicating areas of origin) for genera of elapids of northeastern Australia. Numbers in parentheses refer to the the number of species from each genus from the proposed centres of diversity *vs* total number of species for that genus.

northern and/or eastern	western and/or central	southern
Acanthophis (2/3)	*Denisonia* (2/4)	*Notechis* (1/2+)
Cacophis (4/4)	*Pseudonaja* (5/6)	
Cryptophis (2/2)	*Simoselaps* (8/10)	
Demansia (5/6)	*Suta* (1/1)	
Furina (2/2)	*Unechis* (3/6)	
Glyphodon (2/2)		
Hemiaspis (2/2)		
Hoplocephalus (2/3)		
Oxyuranus (2/2)		
Pseudechis (4/5)		
Tropidechis (1/1)		
Vermicella (2/2)		

Five species of elapid snakes occur in rainforests of northeastern Queensland. All of these have northern limits of occurrence near the southern part of Cape York Peninsula (Cooktown or Cairns area) and none are represented in New Guinea. Conversely *Micropechis ikaheka* (also in gallery forests); *Aspidomorphus lineaticollis, A. schlegeli,* and *A. muelleri* (also in gallery forests); *Parapistocalamus hedigeri; Salomonelaps par* (only from the northern Solomons); *Toxicocalamus bruegersi, T. holopelturus, T. longissimus, T. misimae, T. preusii, T. spilolepidotus, T. stanleyanus* and *T. loriae* (which inhabits areas of secondary growth as well as rainforest) of rainforests of New Guinea (F. Parker, pers. comm.) have not colonised similar habitat in northern Australia. Several genera which occur in open forests on Cape York Peninsula have also not apparently colonised New Guinea - *Furina, Cacophis, Hoplocephalus, Simoselaps, Suta* and *Vermicella.*

The following species of elapids occur in rainforests in the eastern tropics and subtropics - *Hoplocephalus stephensii* (Map 37), *Notechis scutatus* (Map 41), *Pseudechis porphyriacus* (Map 49), *Cacophis* sp. nov., *Cacophis krefftii* (Map 6), *Cacophis squamulosus* (Map 7), *Cryptophis nigrescens* (Map 8), *Hemiaspis signata* (Map 34) and *Tropidechis carinatus* (Map 68). Most of these may be termed 'almost obligatory' rainforest species, at least in the northern part of their range. In Queensland, *H. stephensii, N. scutatus, P. porphyriacus, Cacophis* sp. nov., *C. krefftii, C. squamulosus, H. signata* and *T. carinatus* occur mainly in rainforests although they are not confined to them. In northern Queensland, *C. nigrescens* is confined to rainforests. Where these species range beyond rainforests they are invariably associated with other moist forests. This applies especially to the occurrence in both coastal heathland and rainforest (in southern Queensland) of *N. scutatus, T. carinatus, H. stephensii* and *H. signata*. Not surprisingly, those species which are strongly (if not invariably) associated with rainforests have broadly similar disjunct distributions which parallel the occurrence of the rainforests (*e.g. T. carinatus* - Barrington Tops, mideast N.S.W. to Fraser Is., SE Qld and Mt Spec - Mt Lewis, NE Qld; *H. stephensii* - Gosford, N.S.W. to Gympie area, SE Qld and Kroombit Tops, mideast Qld; *C. krefftii* - Gosford, N.S.W. to Cooran Plateau, near Gympie, SE Qld and Crediton area, mideast Qld).

Pseudechis porphyriacus (Map 49) (in Queensland) has been found in both open forests and rainforests in the south, but is now scarce in coastal areas outside rainforests due, apparently, to the presence of the toxic Cane Toad, *Bufo marinus*, to which it is extremely susceptible. North of the southeast corner of the state, records suggest that *P. porphyriacus* becomes progressively more rainforest dependent. At the northern limits of its occurrence (Mt Hartley and Home Rule, near Cooktown) it is found only in rainforest.

Kikkawa *et al.* (1979) observed that the presumed history of tropical and subtropical rainforest (on fertile soils) is paralleled by that of heaths (on relatively infertile soils). Both are believed to have early (Gondwanan) origins and to have been widespread. In response to Tertiary climatic fluctuations both alternately expanded and contracted. Both habitats are presently fragmented and 'contracted'. Their close historical association probably accounts for the high number of reptile species common to both. The distribution of such species is presumably more dependent upon moisture, substrate and micro-habitat features (such as availability of hollow logs) than on canopy height, cover or forest type. Thus more adaptable heath species have been able to colonise rainforests and *vice versa*. Amongst such species are the elapids, *H. signata, H. stephensii, T. carinatus* and *N. scutatus*.

One open-forest species has a markedly disjunct distribution pattern. *Hoplocephalus bitorquatus* (Map 35), a snake of dry coastal areas occurs widely in New South Wales (from the Sydney area north) and central Queensland (as far north as the Rockhampton area). An isolated population of this species also occurs in the Cairns area. *Simoselaps warro* (Map 66), a species of dry coastal northern areas (and a representative of what appears to be an essentially western genus) also appears to have a disjunct distribution. Such is not the case, however. *S. warro* is well known between Mareeba, Mt Surprise and Townsville and on central Cape York Peninsula. The type specimen of this species (QM J188) was allegedly collected approximately 800 km south of Townsville near the present site of Miriam Vale, prior to 1884. As no other southern specimens of this species have been collected despite intensive searching, and as other records of Charles De Vis (who described *S. warro*) are not without error, it seems reasonable to doubt that *S. warro* occurs south of the Townsville area, despite the accepted type locality.

Coastal Queensland is generally moist. There are, however, relatively low rainfall belts on the coast in the vicinity of Cooktown, Townsville, and Rockhampton - Gladstone. The 1200 mm (*i.e.* 47") isohyet nears the coast at Cooktown and includes the other two regions. It is not surprising to find western, 'dry country' elapids (and other reptiles) in some or all of these areas - (*Demansia torquata* (Map 15), *Pseudechis australis* (Map 45), *Pseudonaja nuchalis* (Map 54), *Simoselaps warro* (Map 66) (Townsville area only) and *Suta suta* (Map 67).

CONCLUSION

The fossil and phylogenetic data on which a full study of the biogeography of the elapids of Australia (including the northeast) are not yet available. Nonetheless, available data point to:

1. recent origins of this group in Australia (Pliocene and Pleistocene fossils only, with current immunological studies by Schwaner suggesting a maximum age of 7 m years);

2. a strong association with New Guinea, the result of recent land links between the two;

3. obligatory rainforest and rainforest/heath species, often with disjunct distributions similar to those of the rainforests;

4. several markedly disjunct patterns of occurrence which may best be interpreted as the result of climatic changes resulting in extinction over parts of the former range of some species; and

5. a 'mixing' of northern and eastern, western and (to a lesser extent) southern 'elements' in the elapids of the northeast of Australia.

ACKNOWLEDGEMENTS

Grey Czechura, Ralph Molnar, Gary Werren, Fred Parker and Charles Tanner have constructively criticised this work and assisted me to sort out ideas. Fred Parker provided me with data on rainforest elapids from New Guinea.

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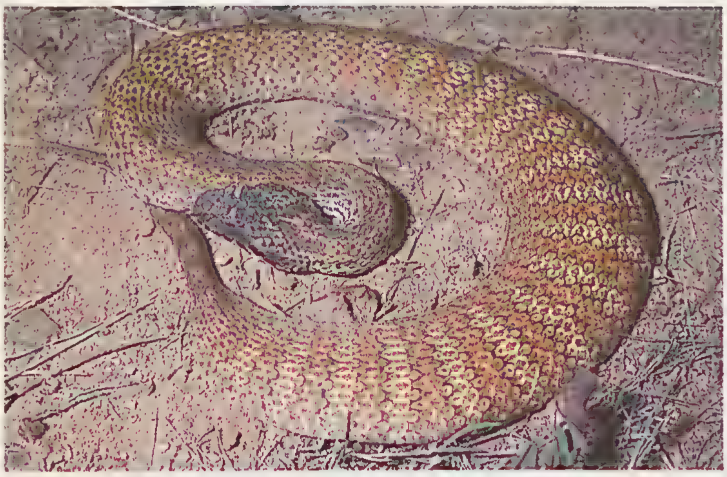
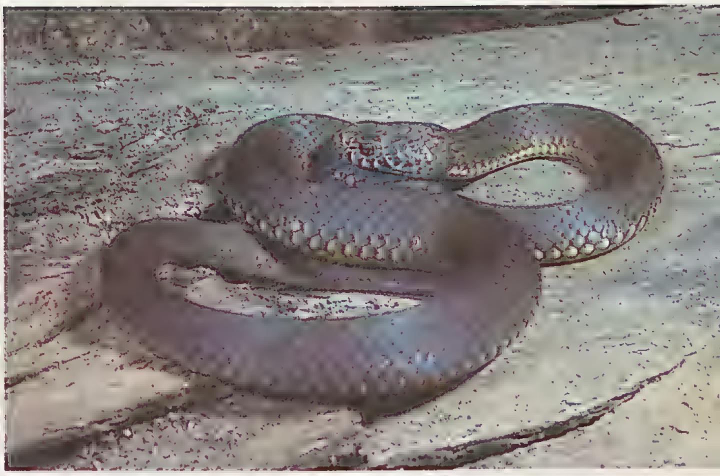
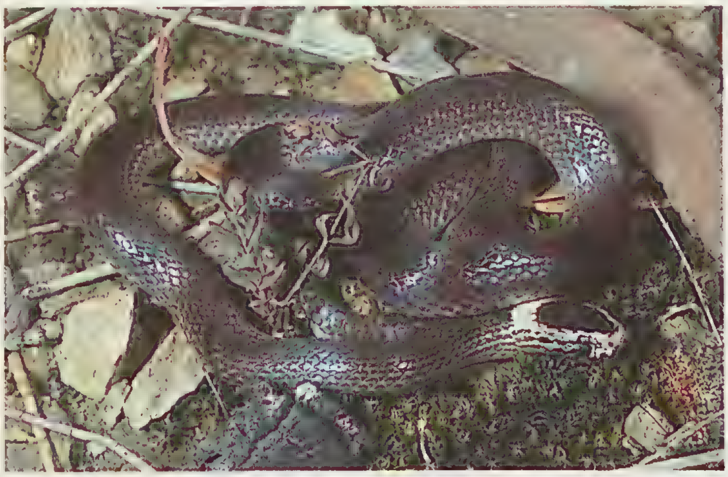
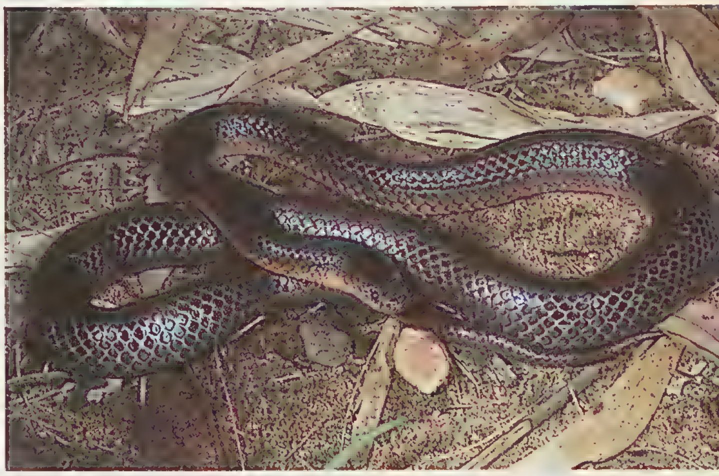
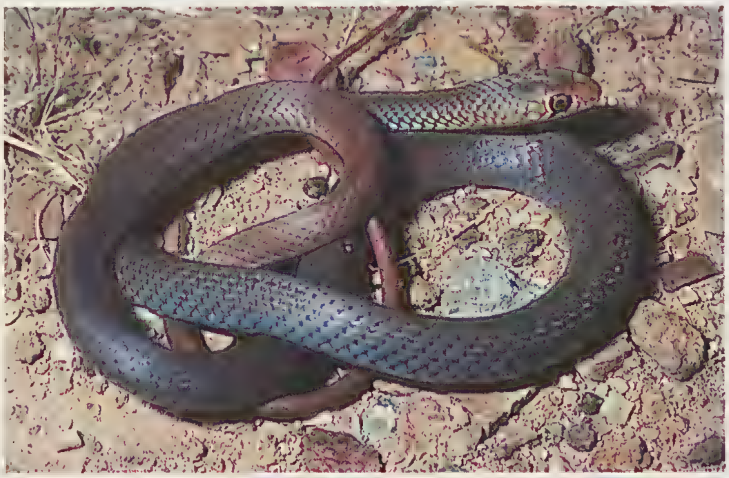
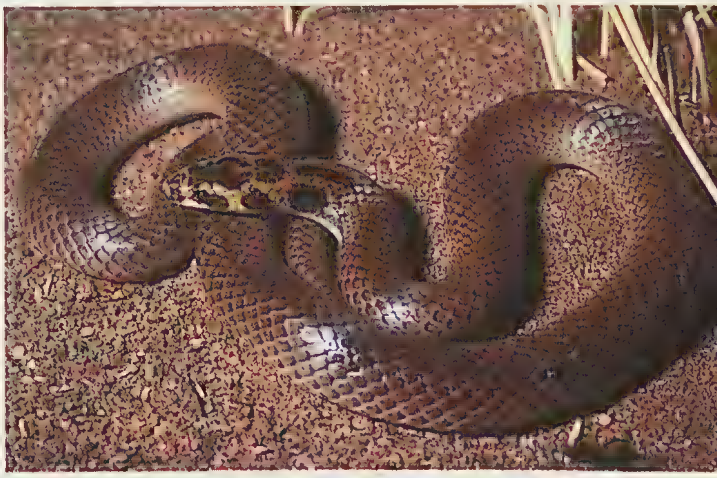












1. *Acanthophis praelongus* – Katherine Gorge, N.T. (R.Jenkins)

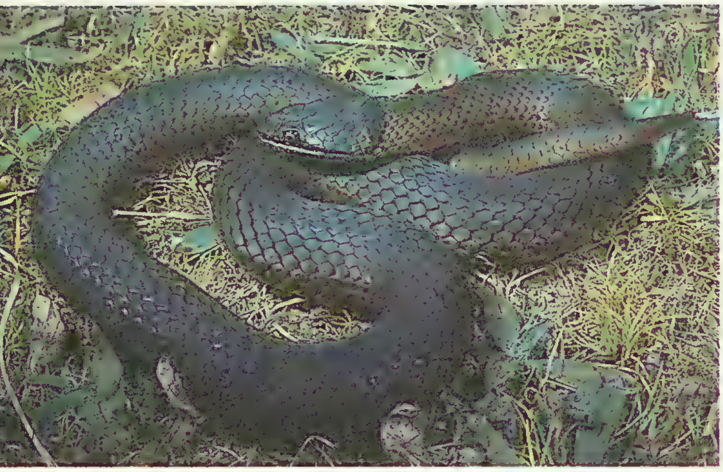
2. *Austrelaps superbus* – Lake Eucumbene, N.S.W. (J.Wombey)

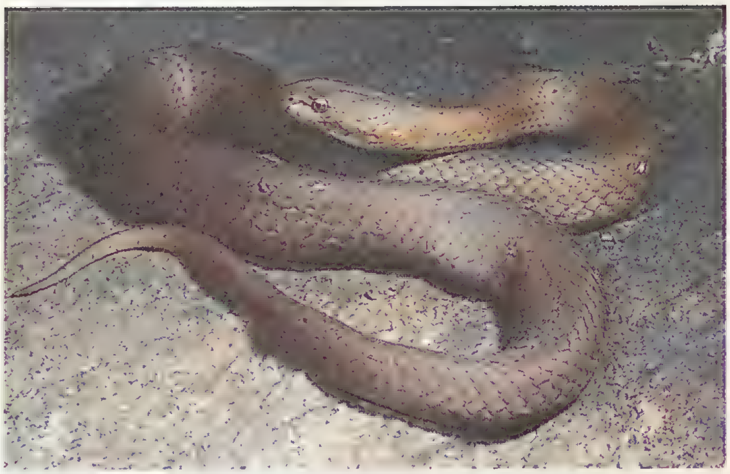
3. *Cacophis harriettae* – Brisbane, Qld (R.Jenkins)

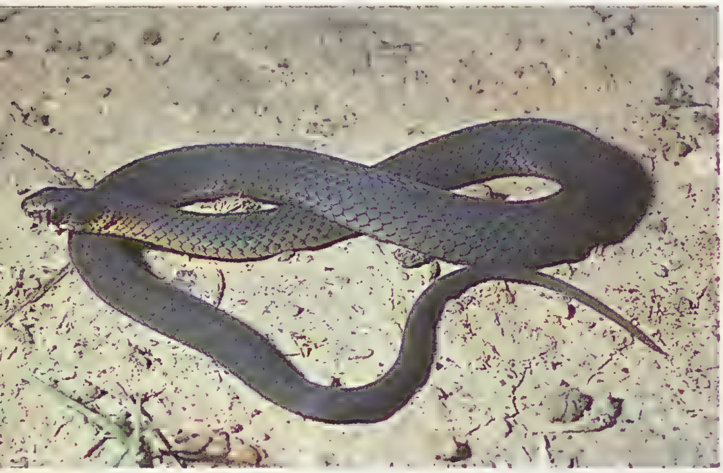
4. *Cryptophis pallidiceps* – Kakadu National Park, N.T. (R.Jenkins)

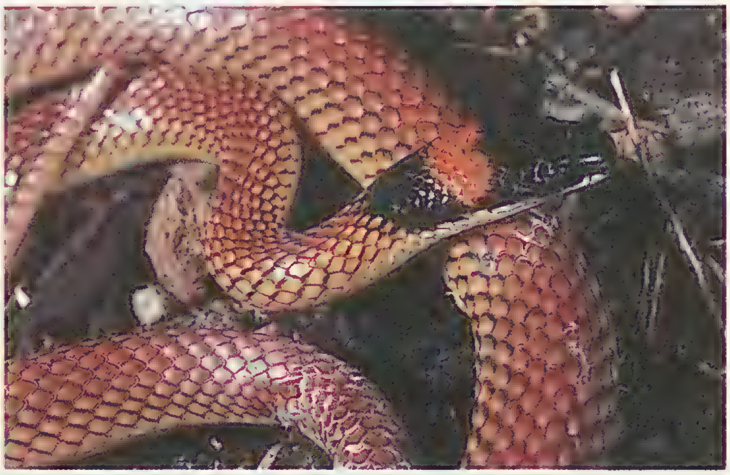
5. *Demansia papuensis* – Darwin, N.T. (R.Jenkins)

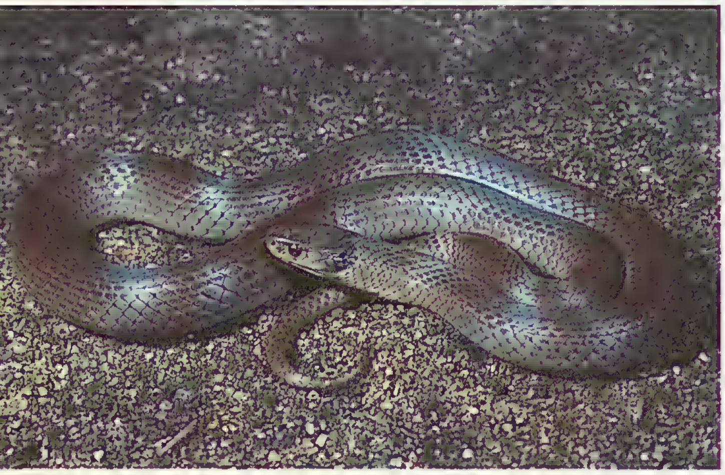
6. *Denisonia punctata* – Daly River, N.T. (R.Jenkins)

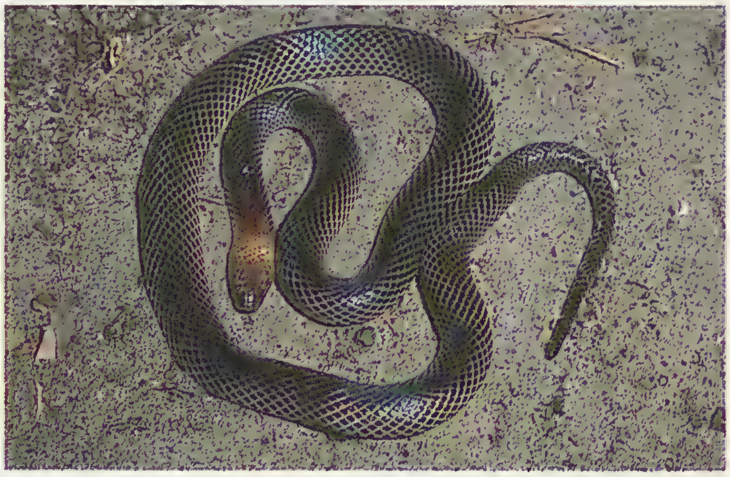












7. *Drysdalia coronata* – Gosnells, W.A. (R.Jenkins)

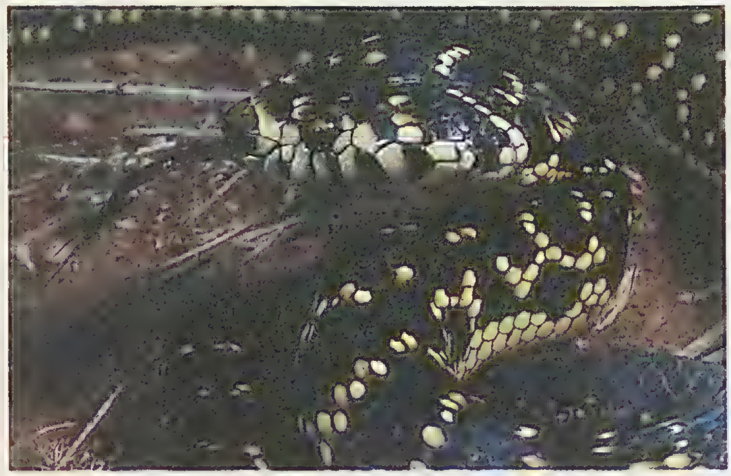
8. *Echiopsis curta* – Cape Leeuwin, W.A. (R.Jenkins)

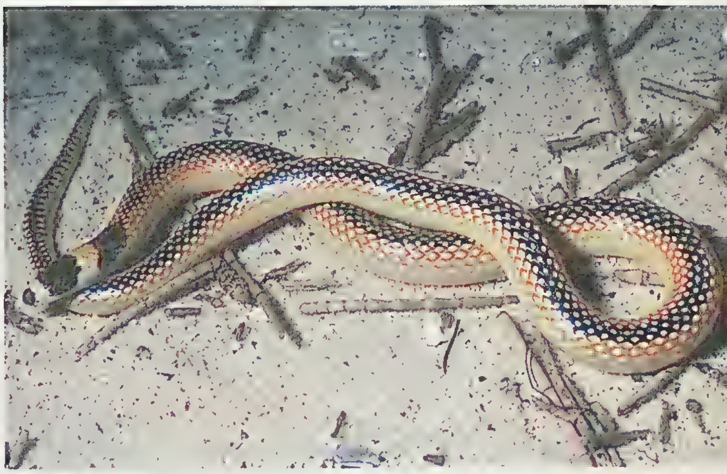
9. *Elapognathus minor* – Albany, W.A. (R.Jenkins)

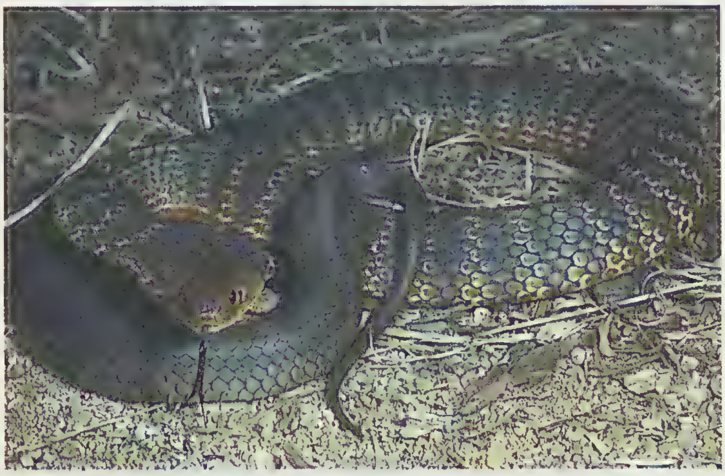
10. *Furina diadema* – Macquarie Marshes, N.S.W. (R.Jenkins)

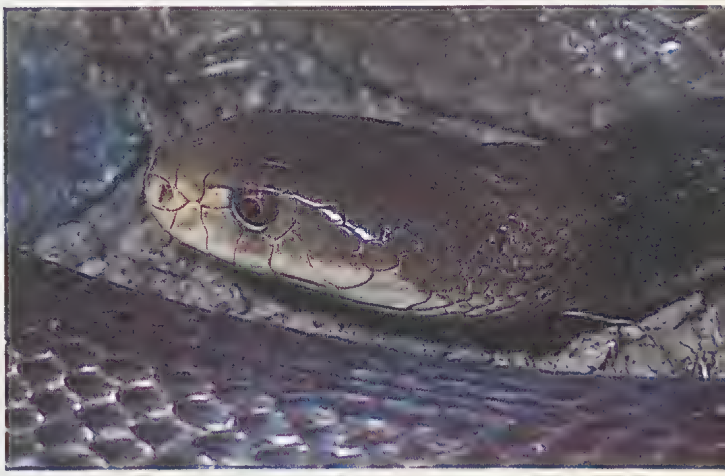
11. *Hemiaspis damelii* – Macquarie Marshes, N.S.W. (R.Jenkins)

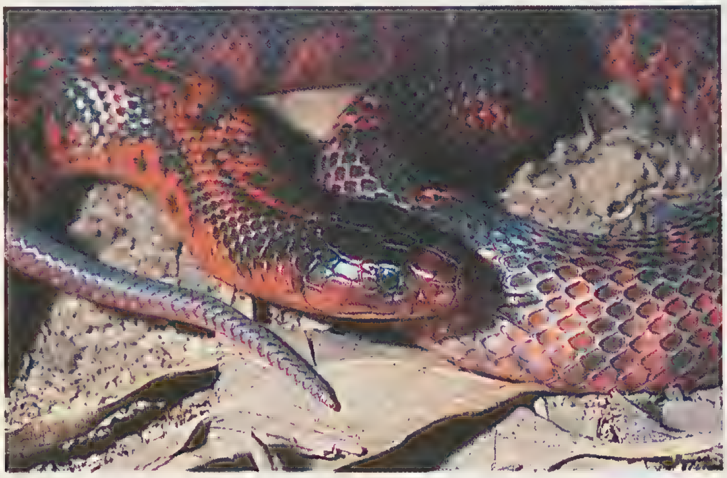
12. *Glyphodon tristis* – Iron Range, N Qld (R.Jenkins)

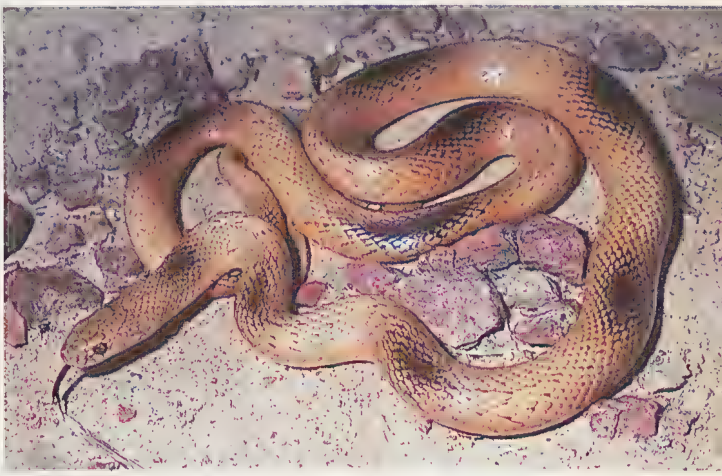












13. *Hoplocephalus bungaroides* – Sydney, N.S.W. (J.Wombey)

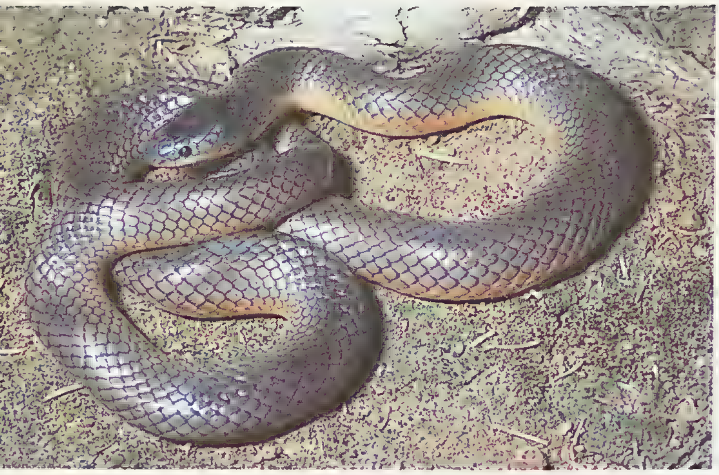
14. *Neelaps calonotus* – Lancelin, W.A. (R.Jenkins)

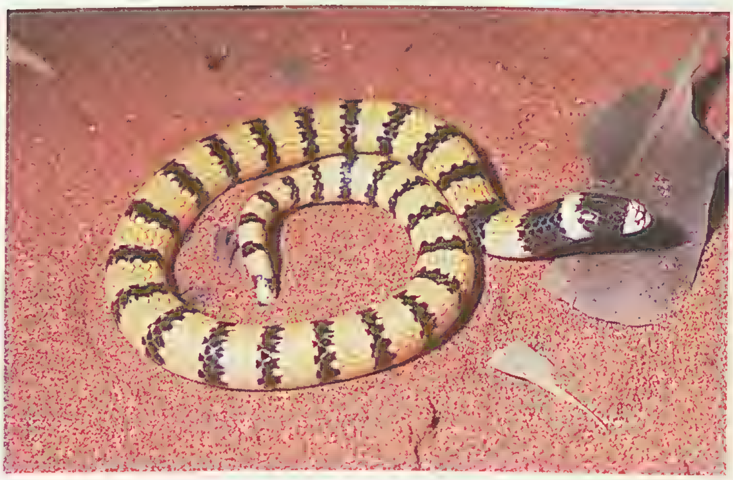
15. *Notechis scutatus* – Rose Lagoon, N.S.W. (J.Wombey)

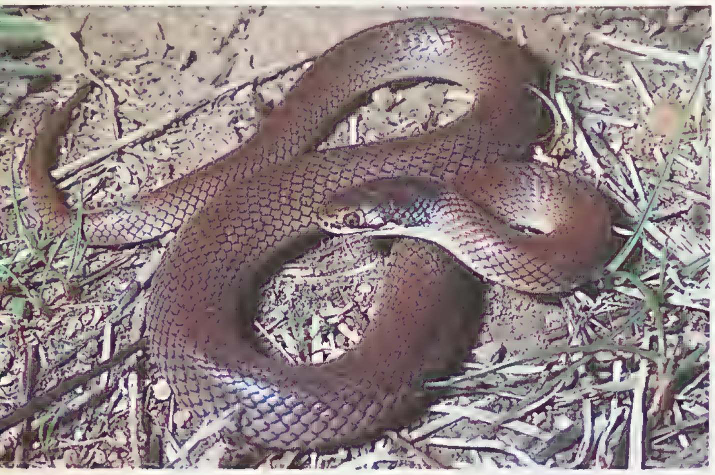
16. *Oxyuranus scutellatus* – Cooktown, Qld (R.Jenkins)

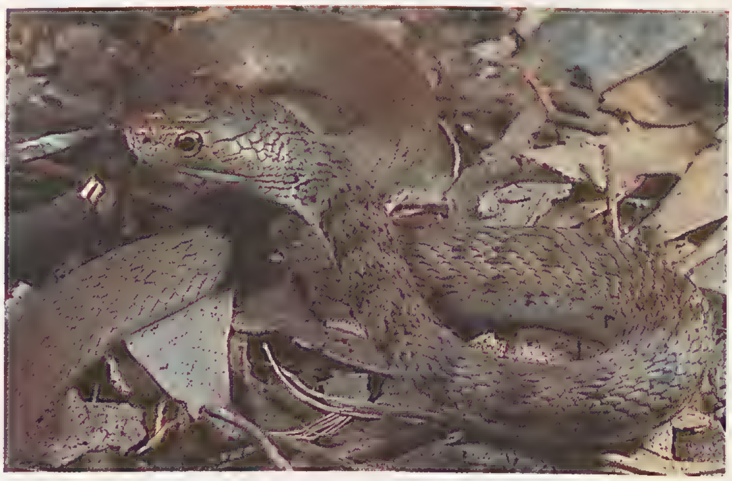
17. *Pseudechis colletti* – Winton, Qld (R.Jenkins)

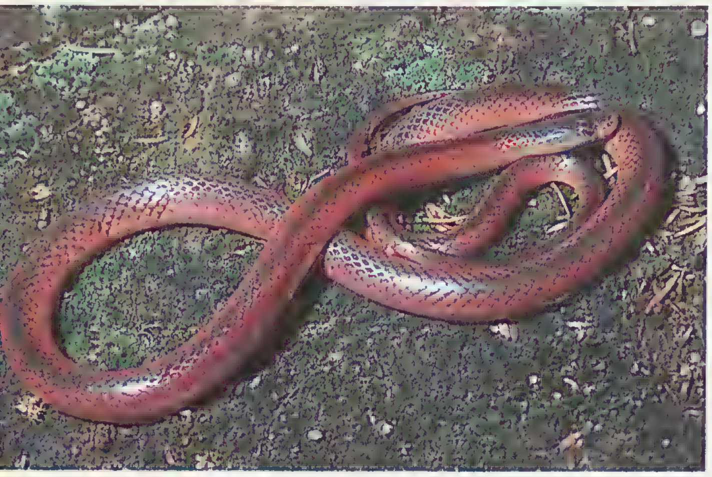
18. *Pseudonaja guttata* – Windorah, Qld (R.Jenkins)

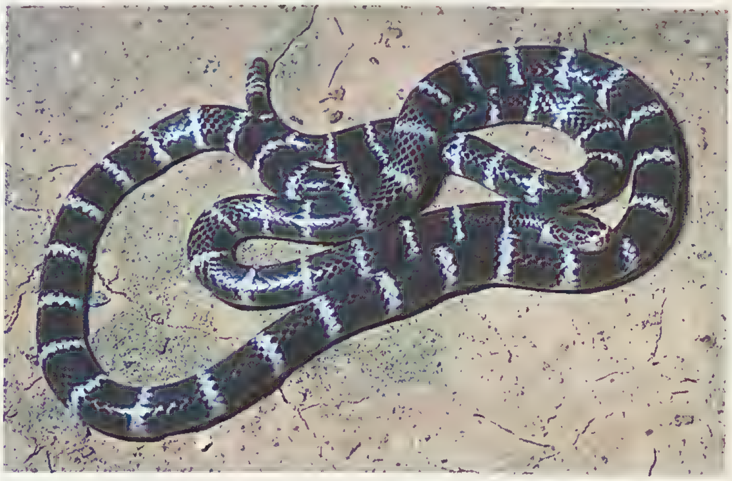












19. *Rhinoplocephalus bicolor* – Albany, W.A. (R.Jenkins)

20. *Simoselaps anomalus* – Sandfire Road House, W.A. (R.Jenkins)

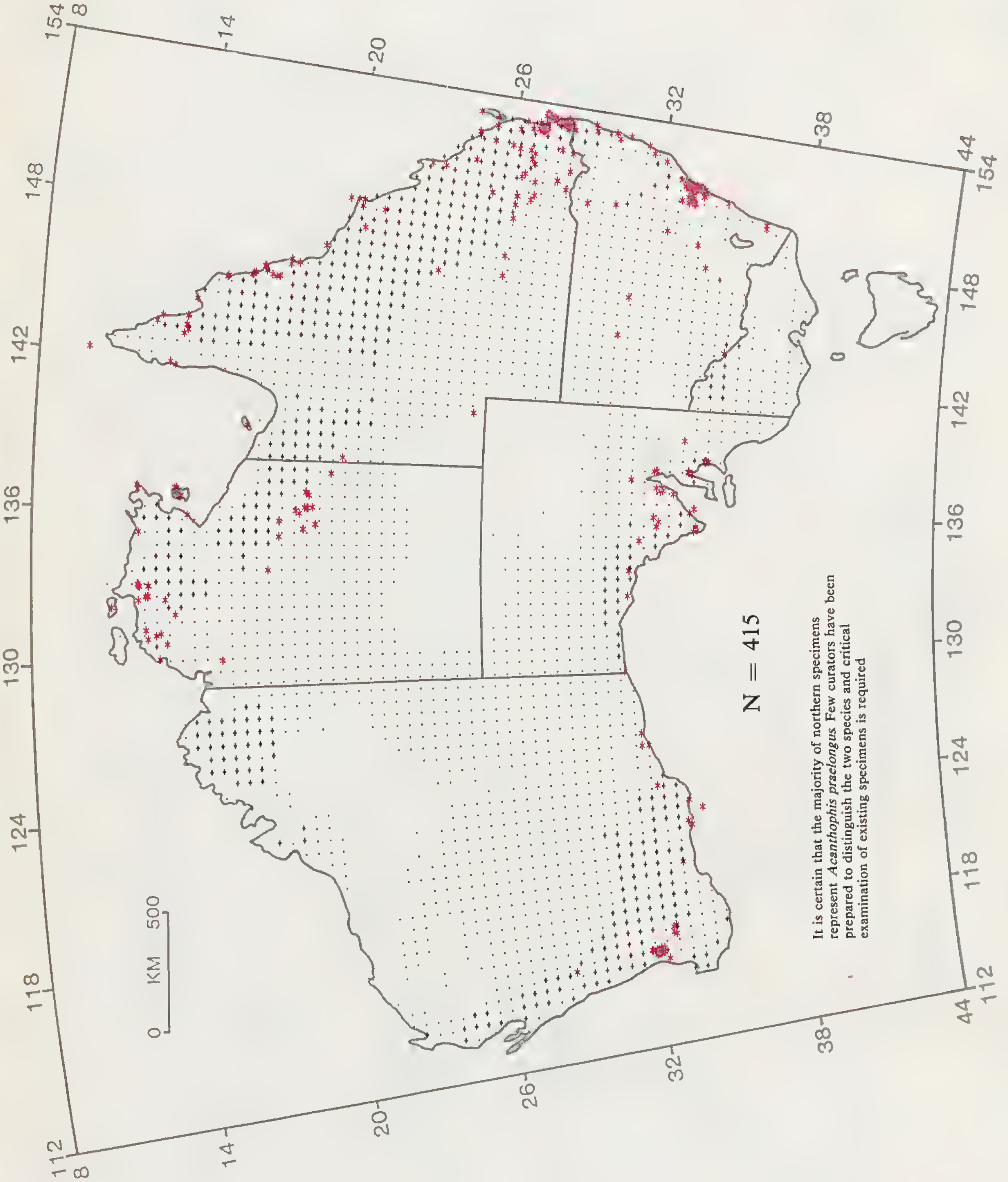
21. *Suta suta* – Carroll, N.S.W. (R.Jenkins)

22. *Tropidechis carinatus* – Mt Glorious, Qld (J.Wombey)

23. *Unechis nigrostriatus* – Granite Gorge via Mareeba, Qld (R.Jenkins)

24. *Vermicella multifasciata* – Humpty Doo, N.T. (R.Jenkins)

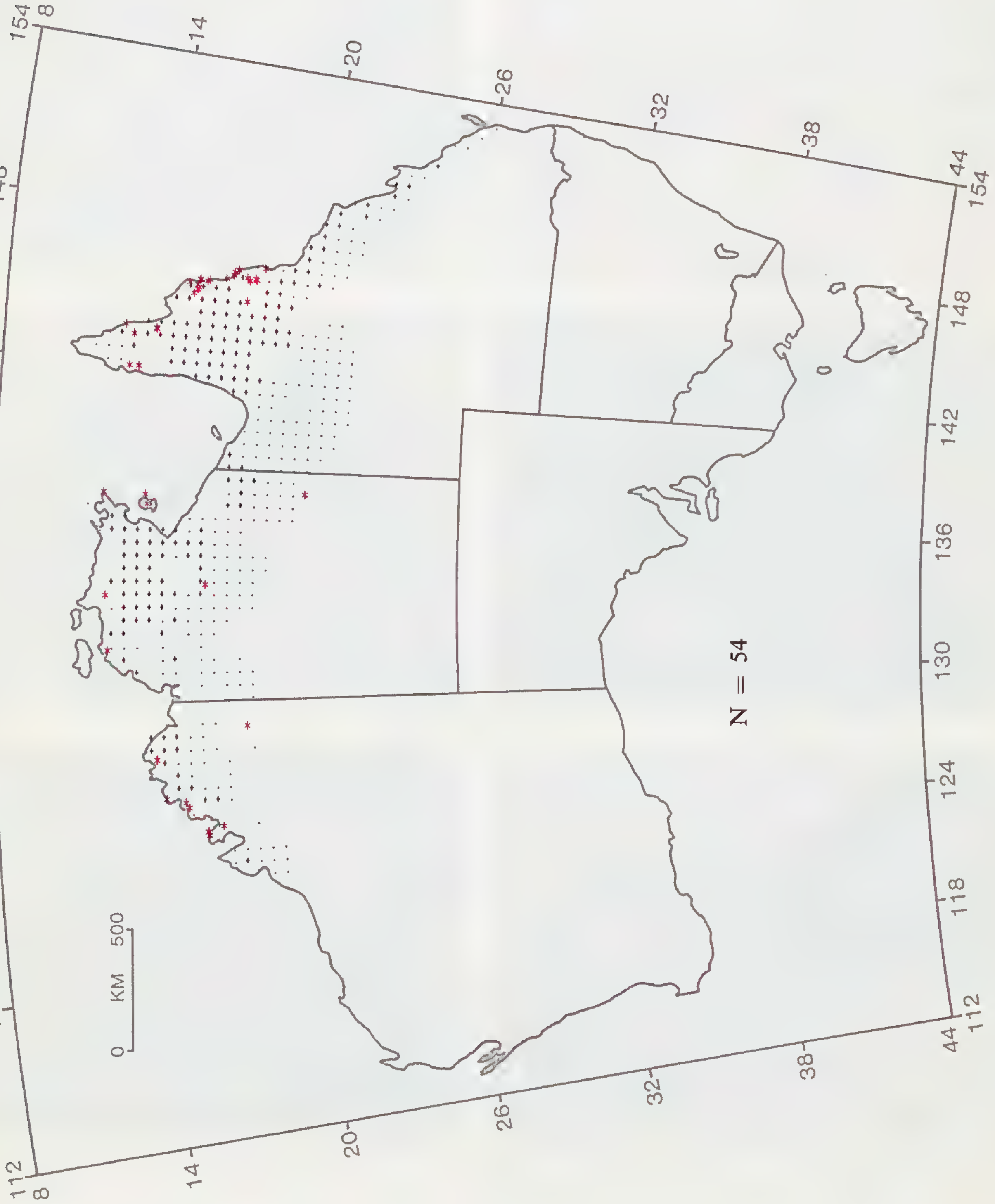
Acanthophis antarcticus **Map 1**



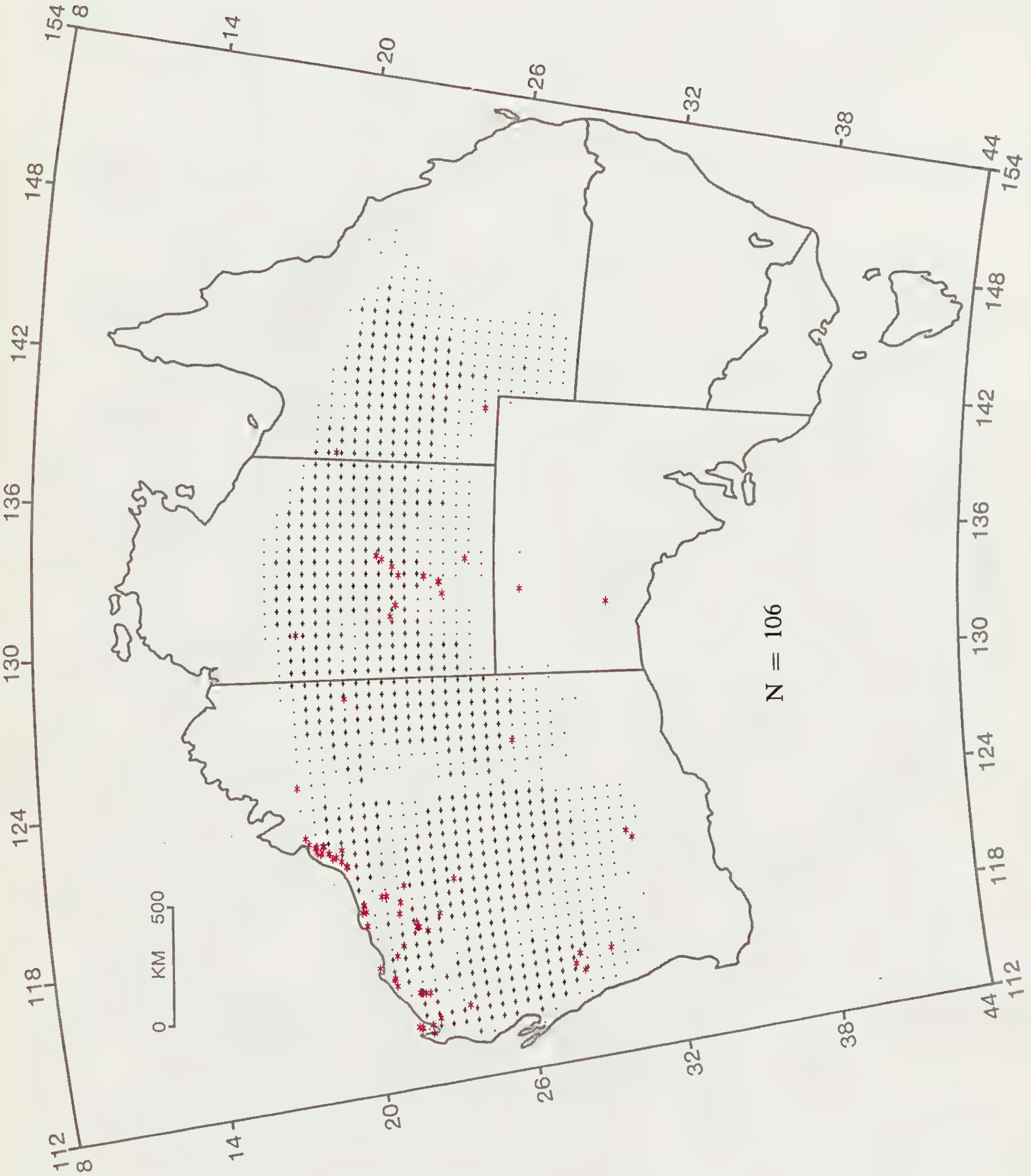
N = 415

It is certain that the majority of northern specimens represent *Acanthophis praelongus*. Few curators have been prepared to distinguish the two species and critical examination of existing specimens is required

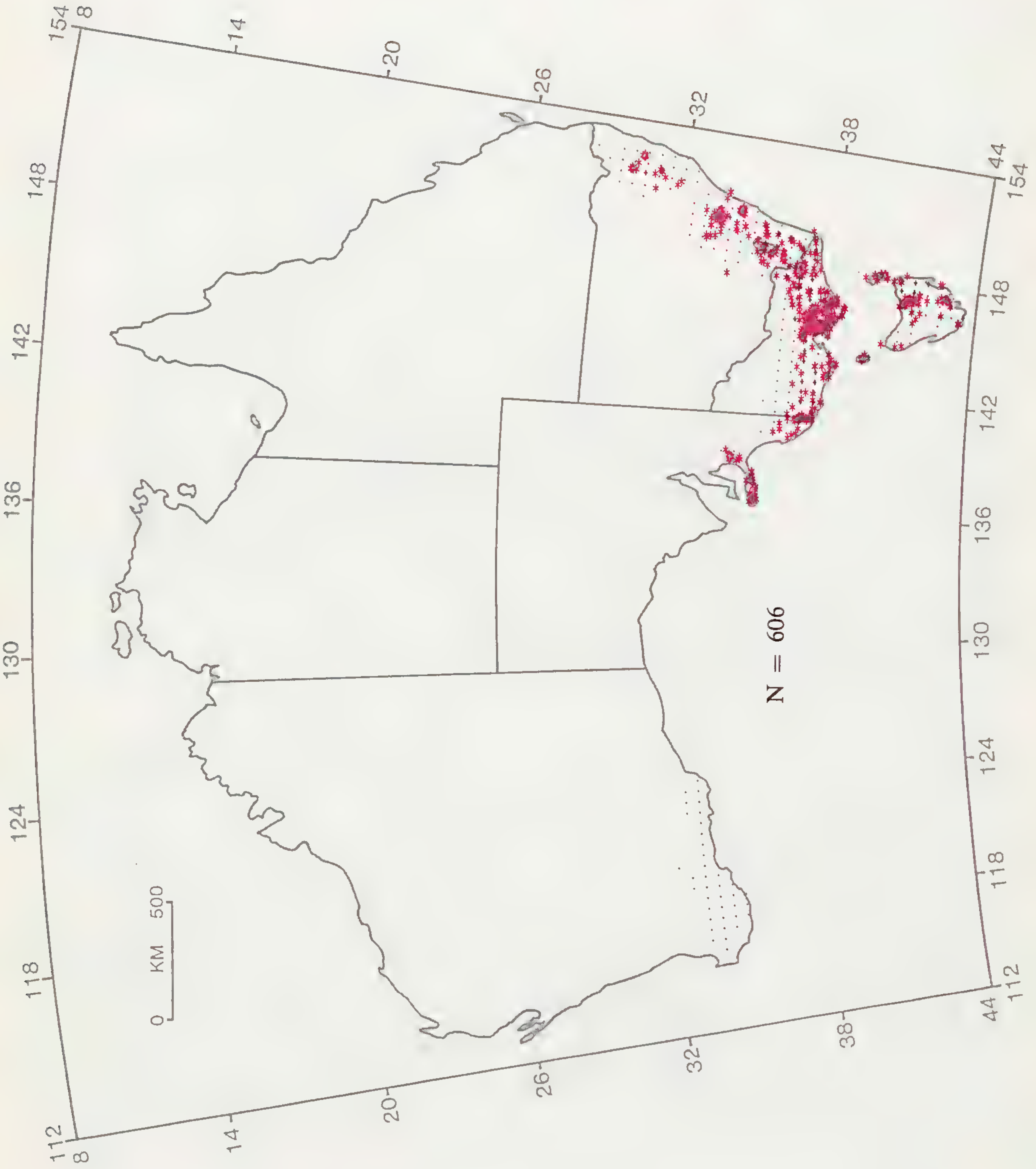
Map 2 Acanthophis praelongus

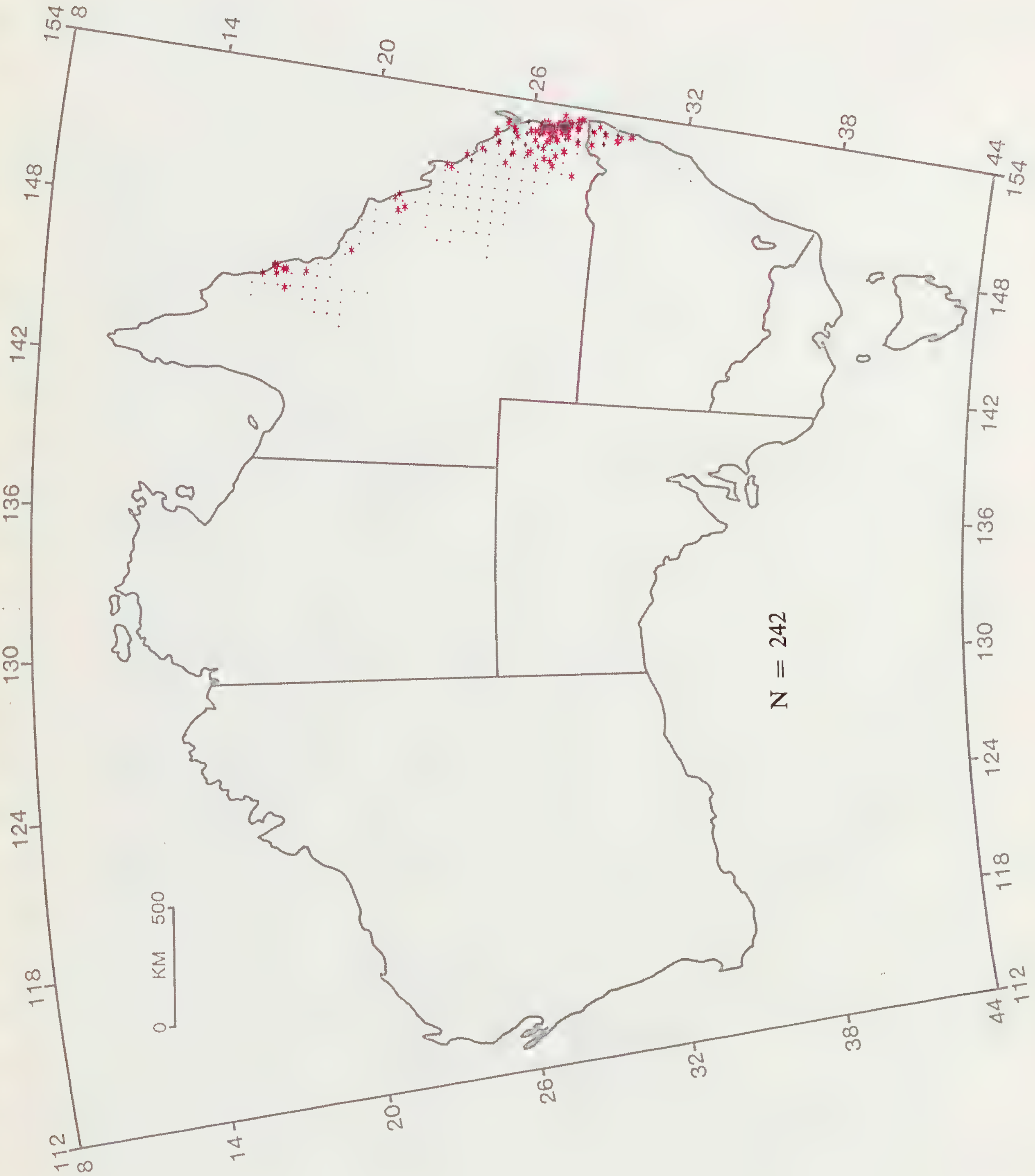


Acanthophis pyrrhus **Map 3**



Map 4 Austrelaps superbus

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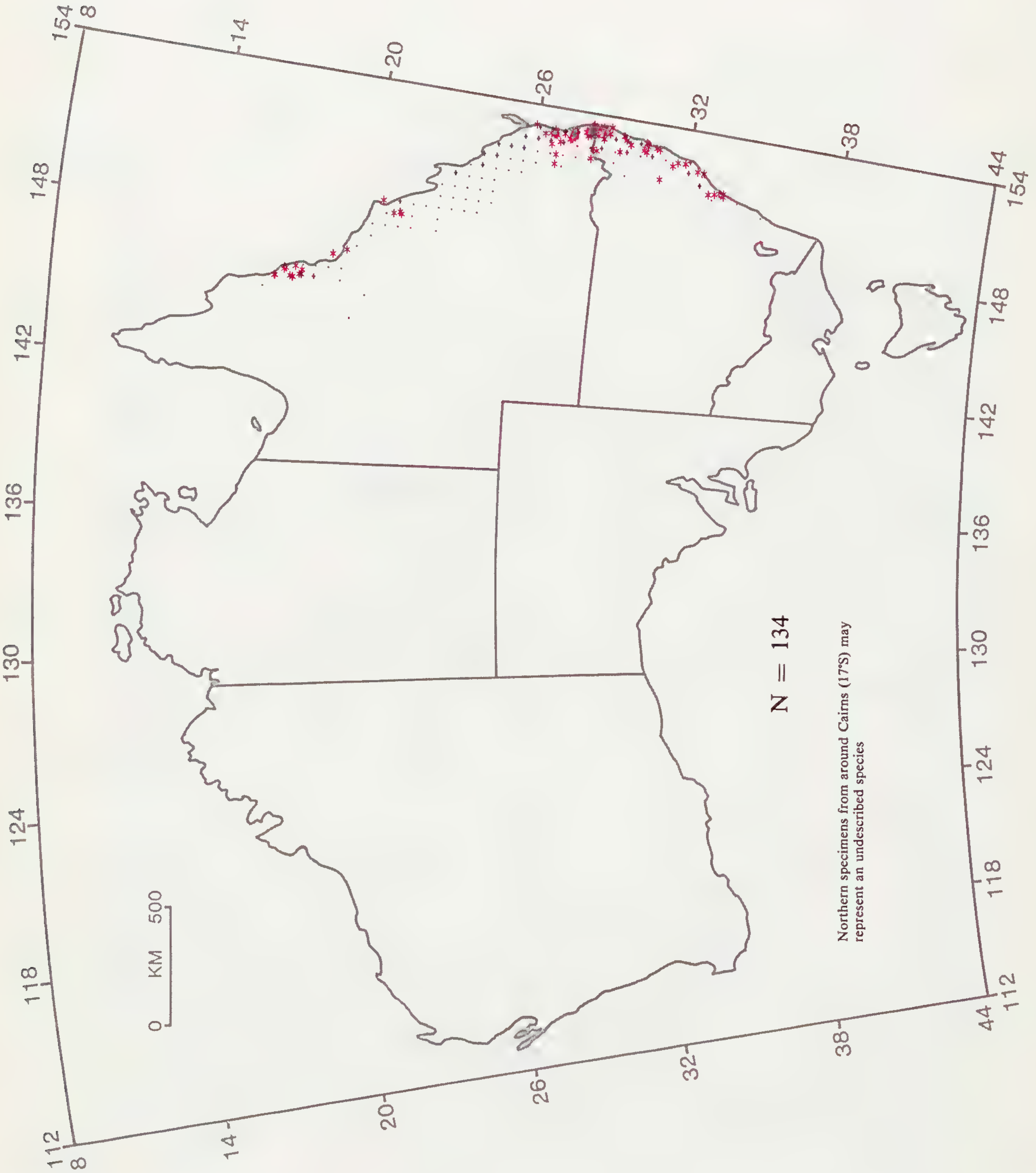
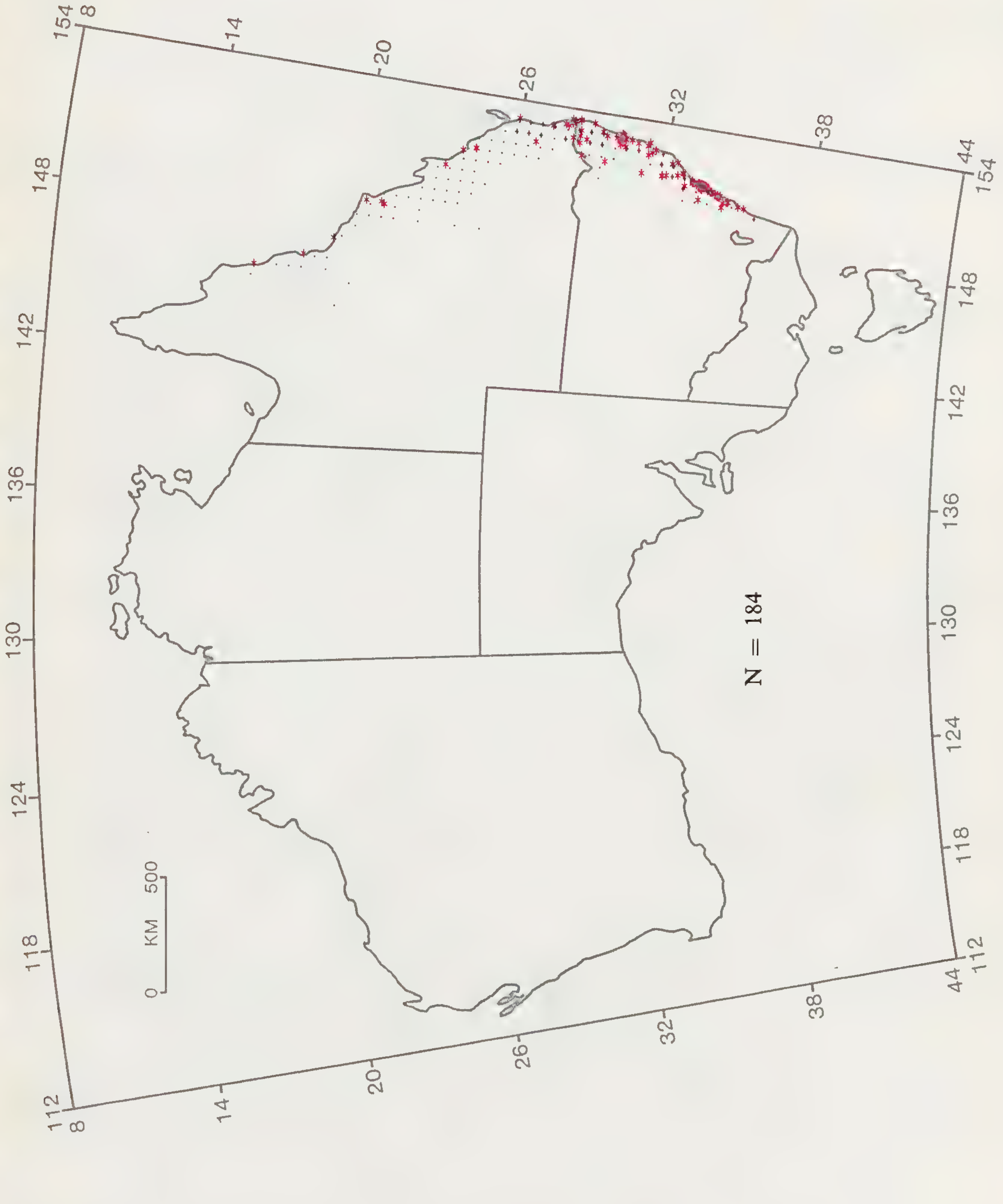
32
38
44
154
148
142
136
130
124
118
112
44
38
32
26
20
14
8
112
118
124
130
136
142
148
0 KM 500
N = 242

Map 6 Cacophis krefftii

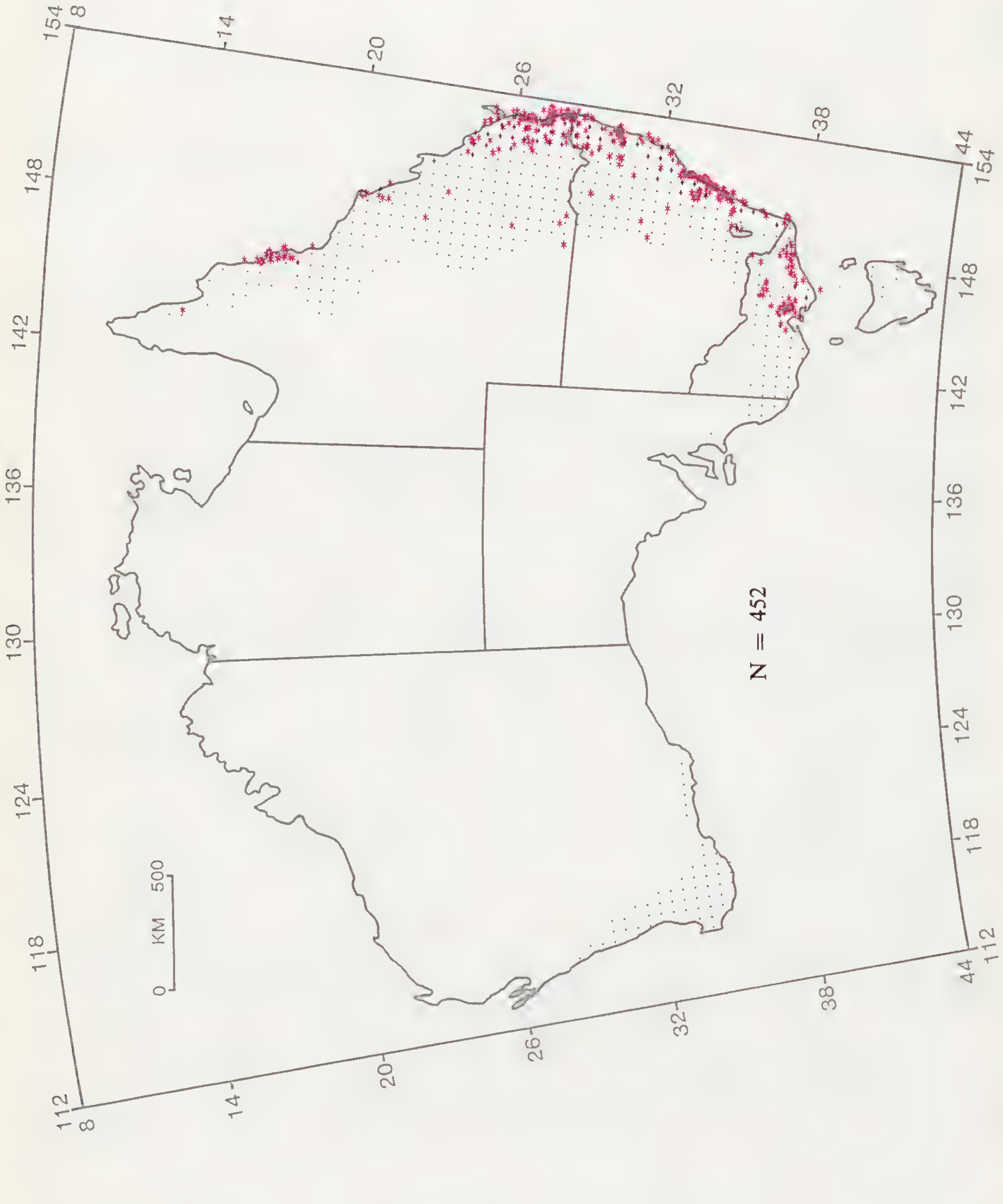


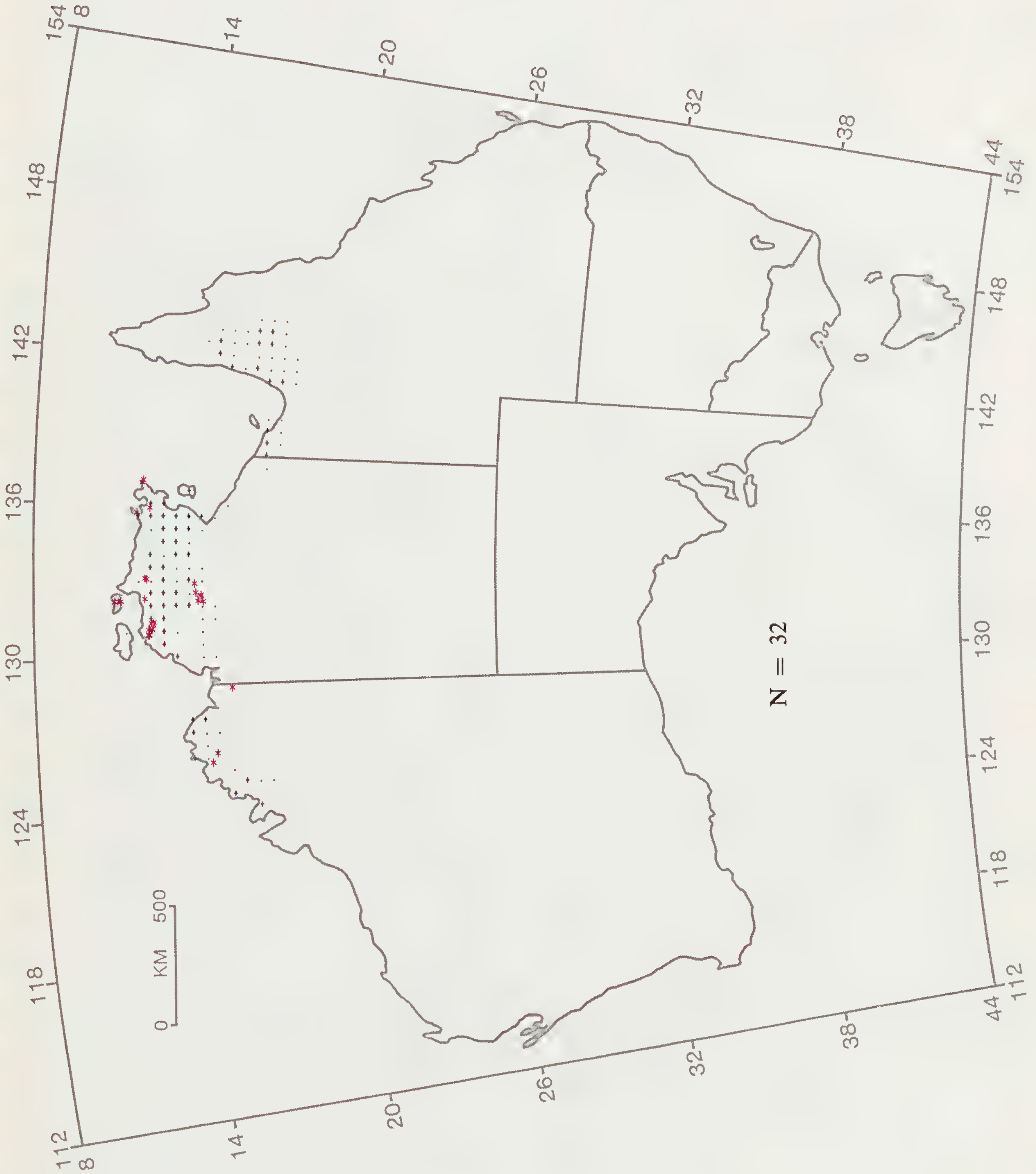
N = 134

Northern specimens from around Cairns (17°S) may represent an undescribed species

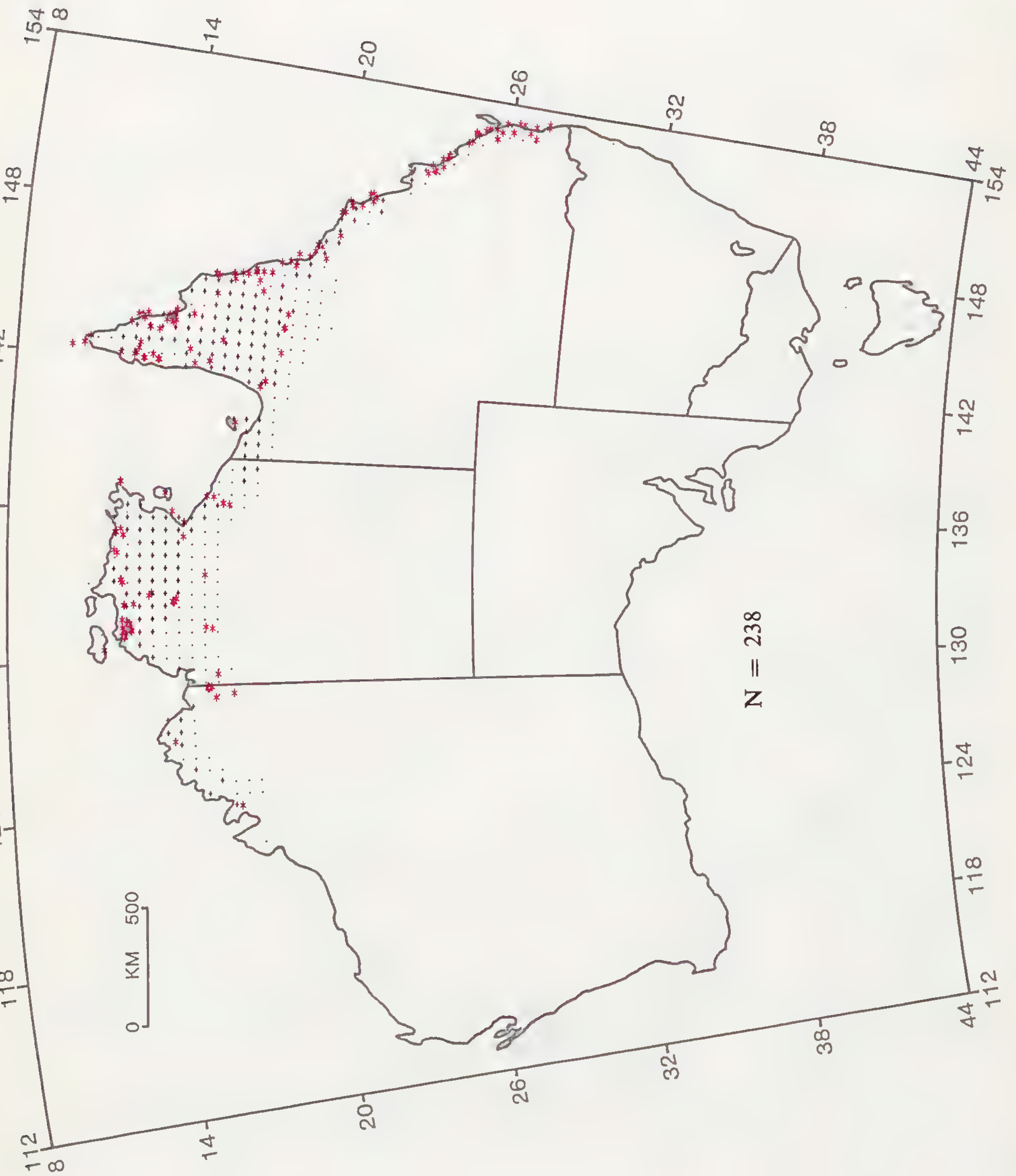

N = 184
0 KM 500
112
118
124
130
136
142
148
154
8
14
20
26
32
38
44

Map 8 Cryptophis nigrescens

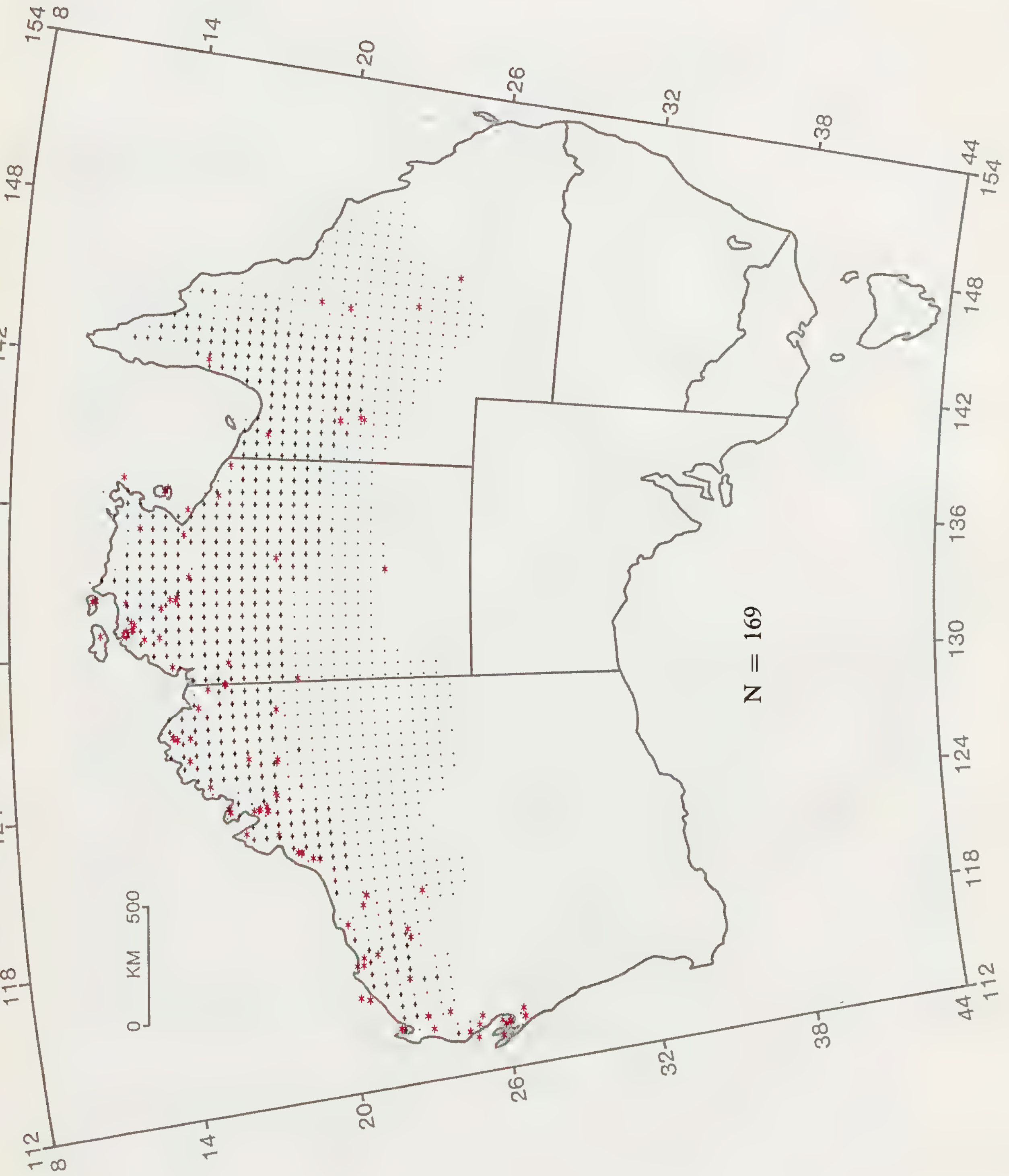



154
8
14
20
26
32
38
44
154
148
142
136
130
124
118
112
44
112
8
14
20
26
32
38
0
KM
500
N = 32

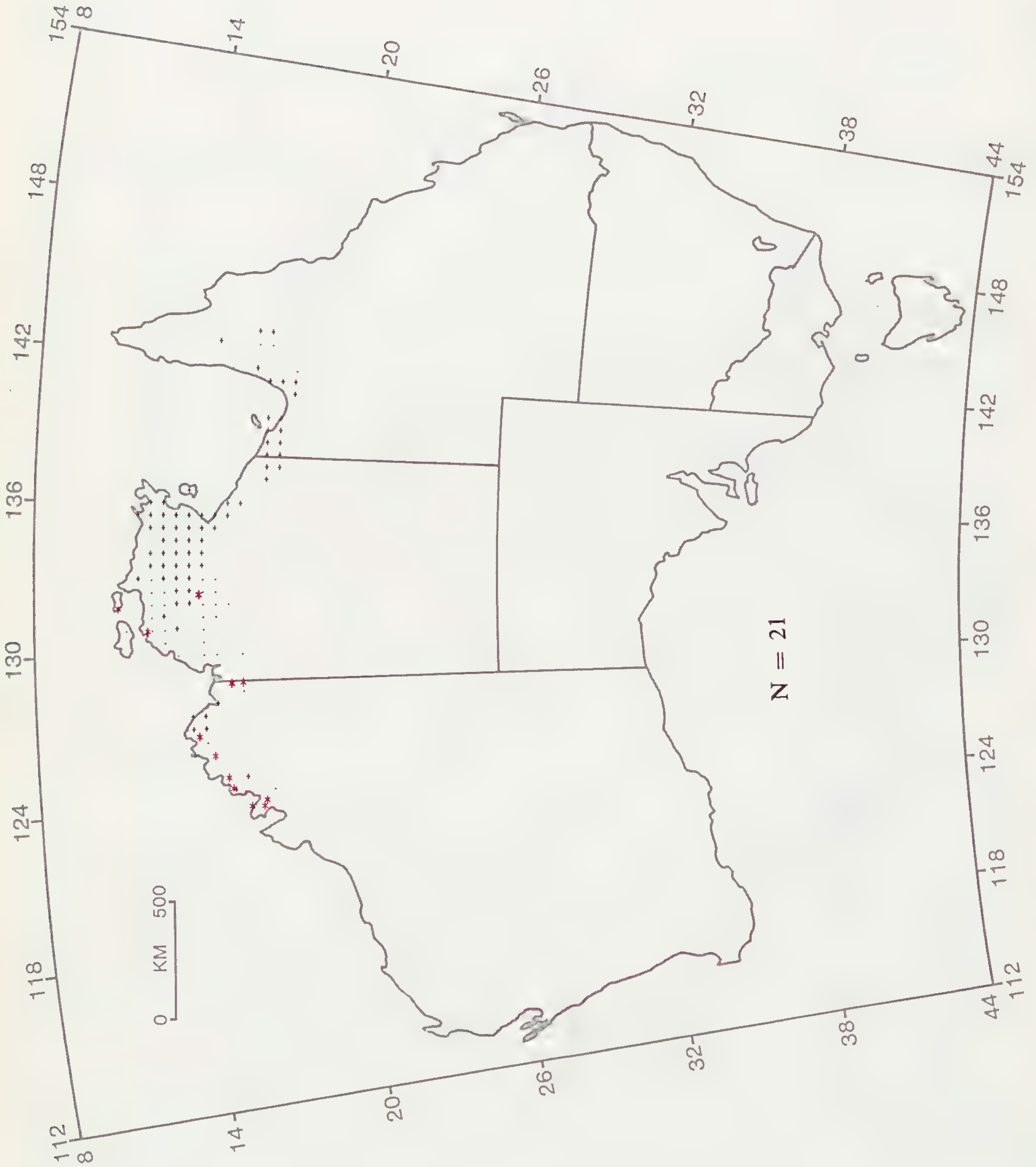
Map 10 Demansia atra



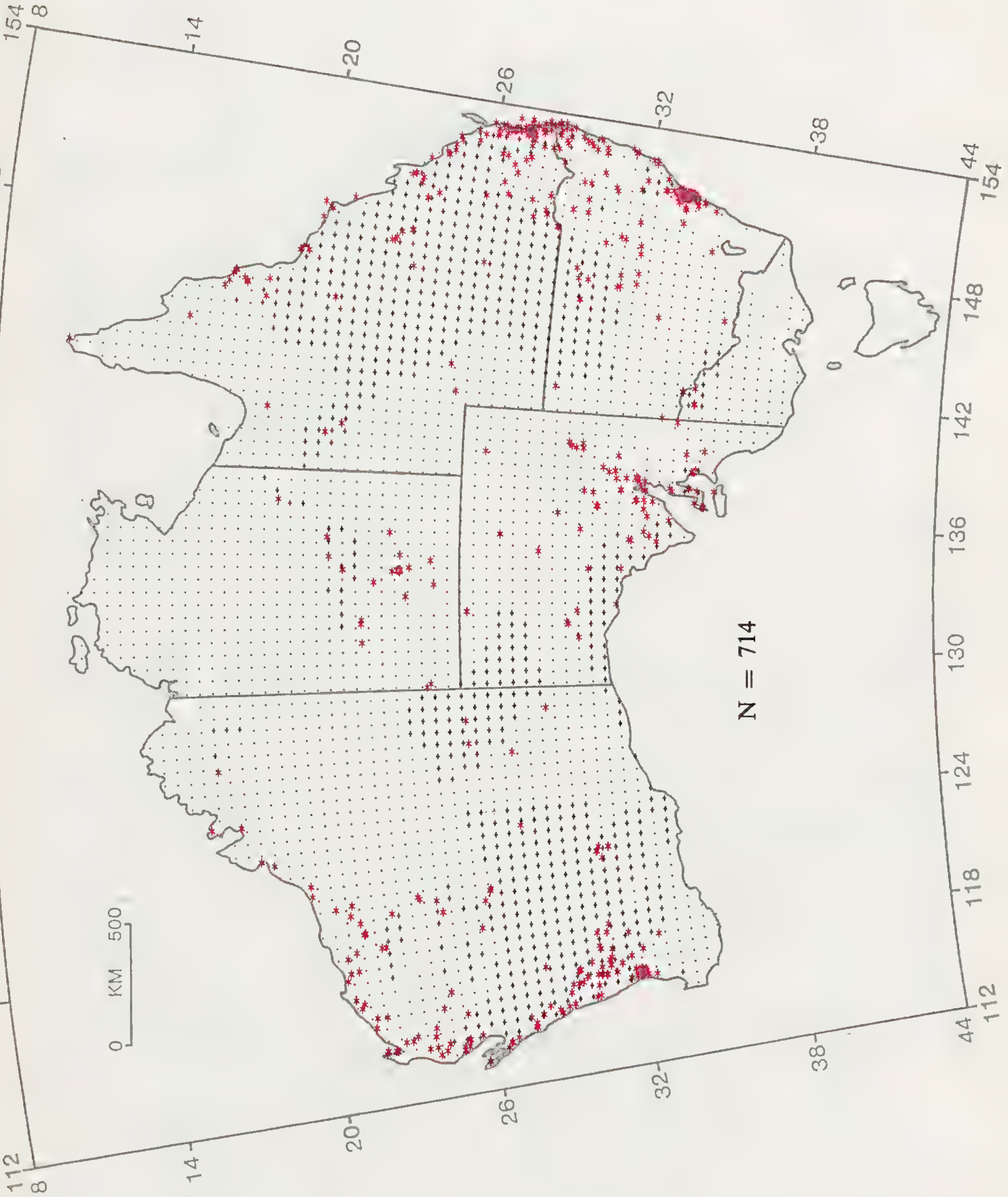
Demansia olivacea **Map 11**



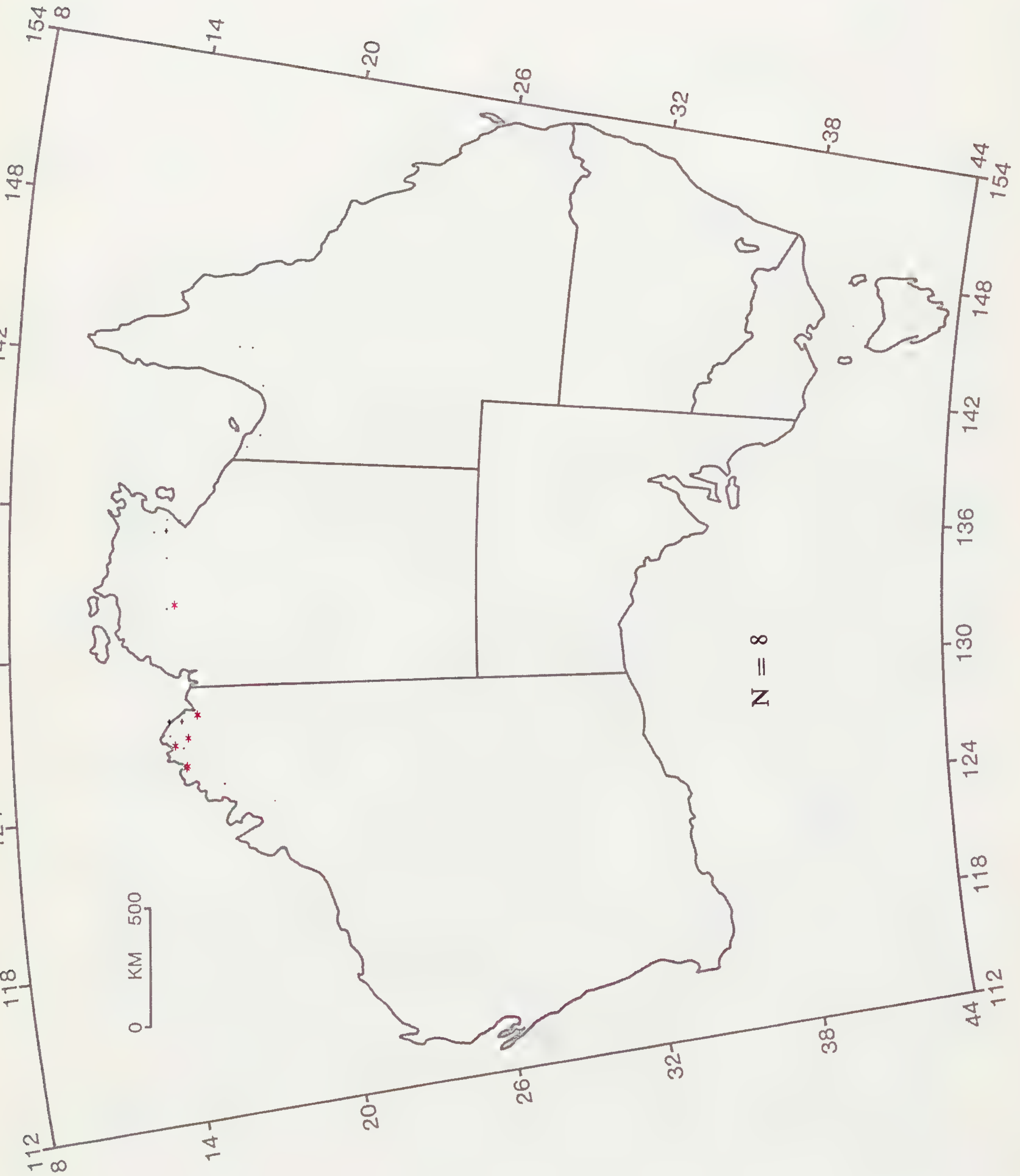
Map 12 Demansia papuensis

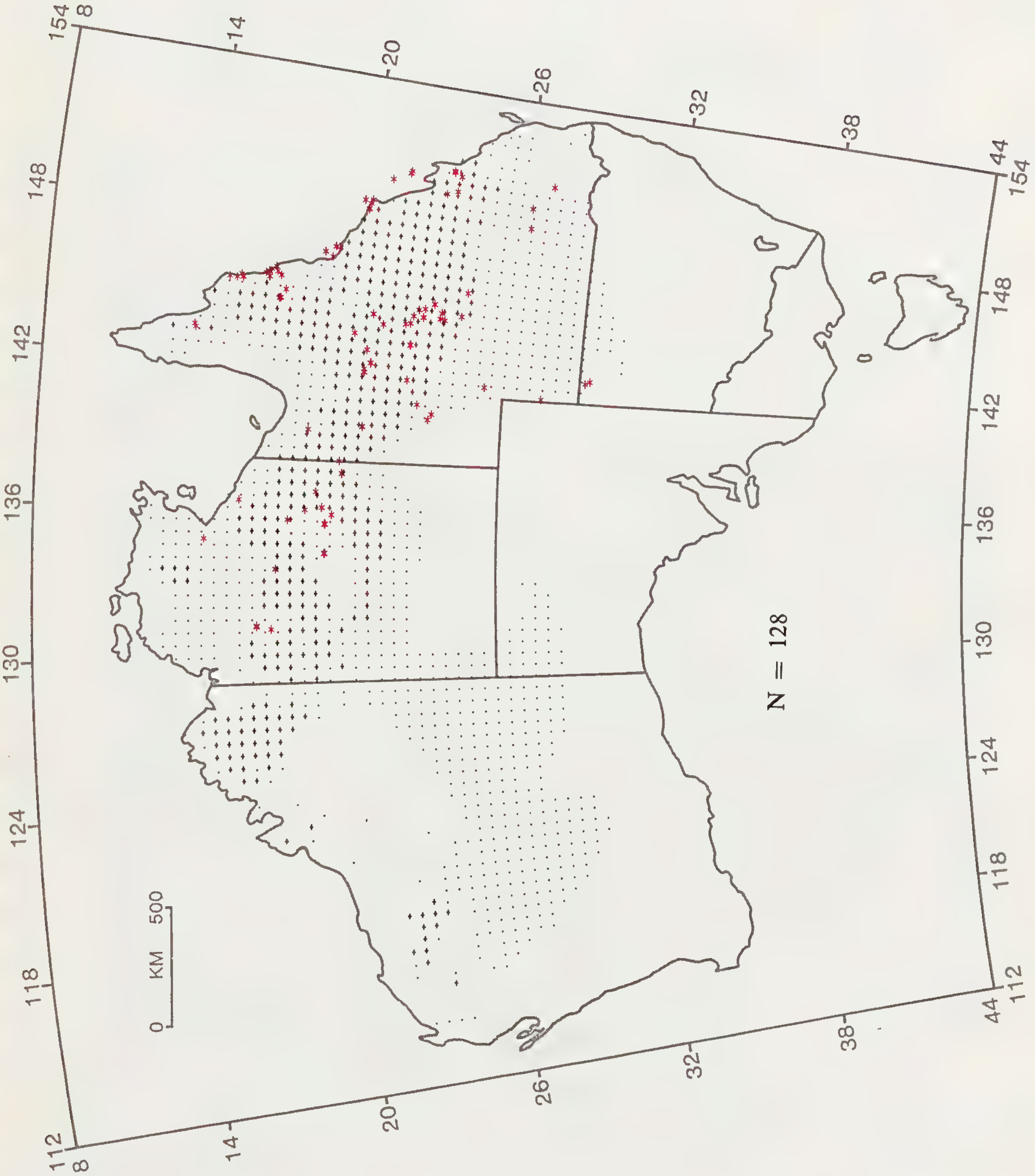


Demansia psammophis **Map 13**

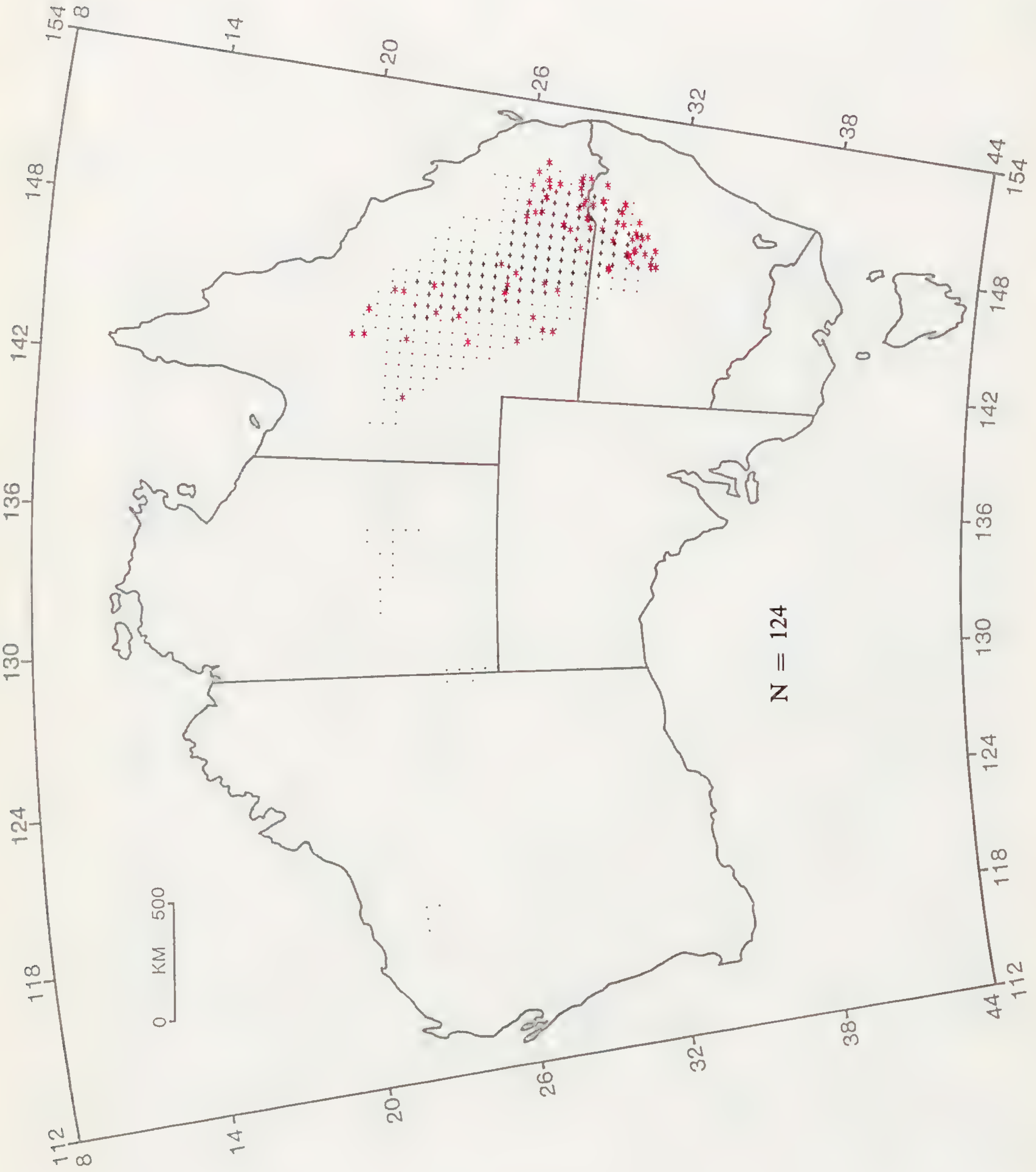


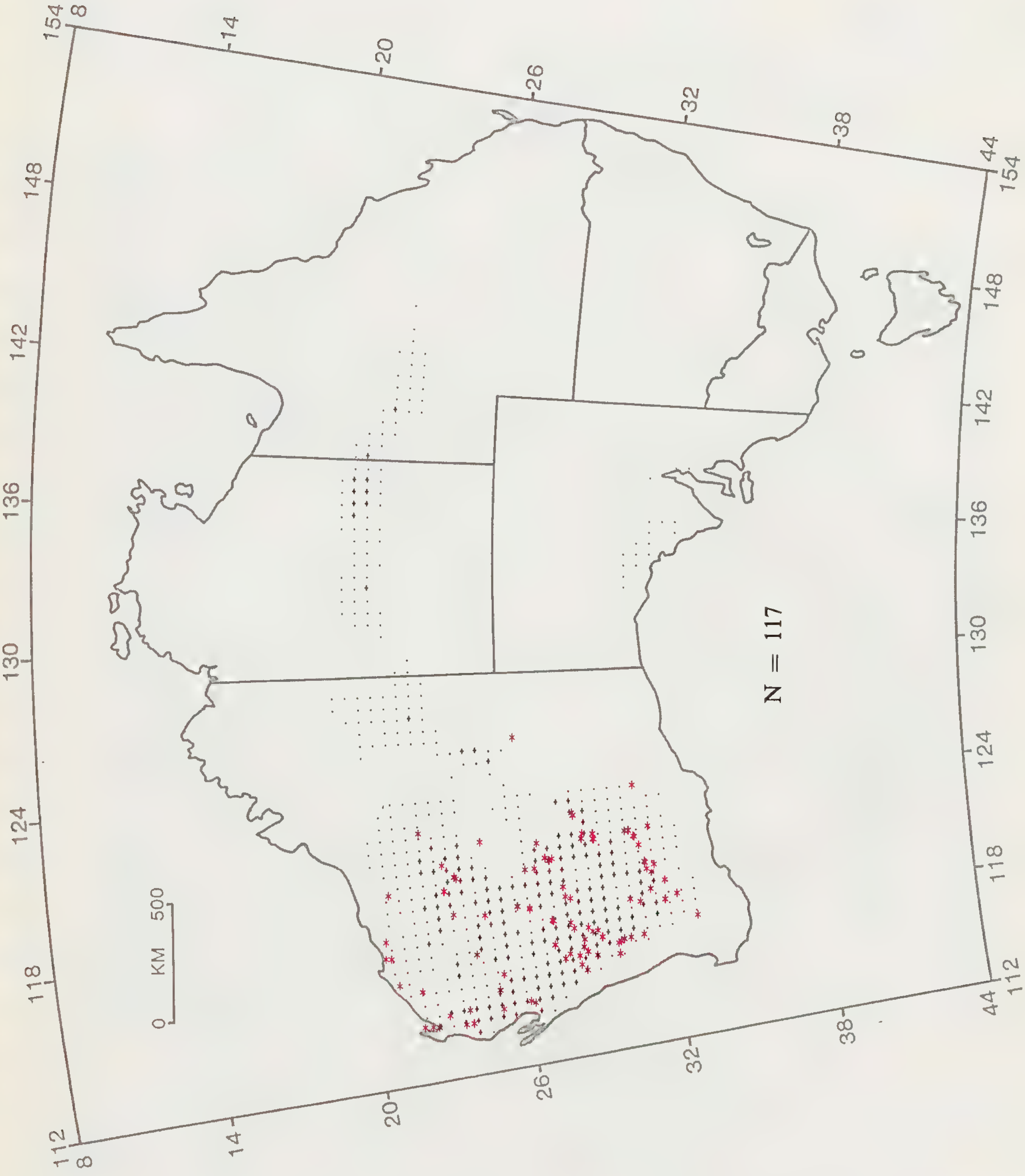
Map 14 Demansia simplex



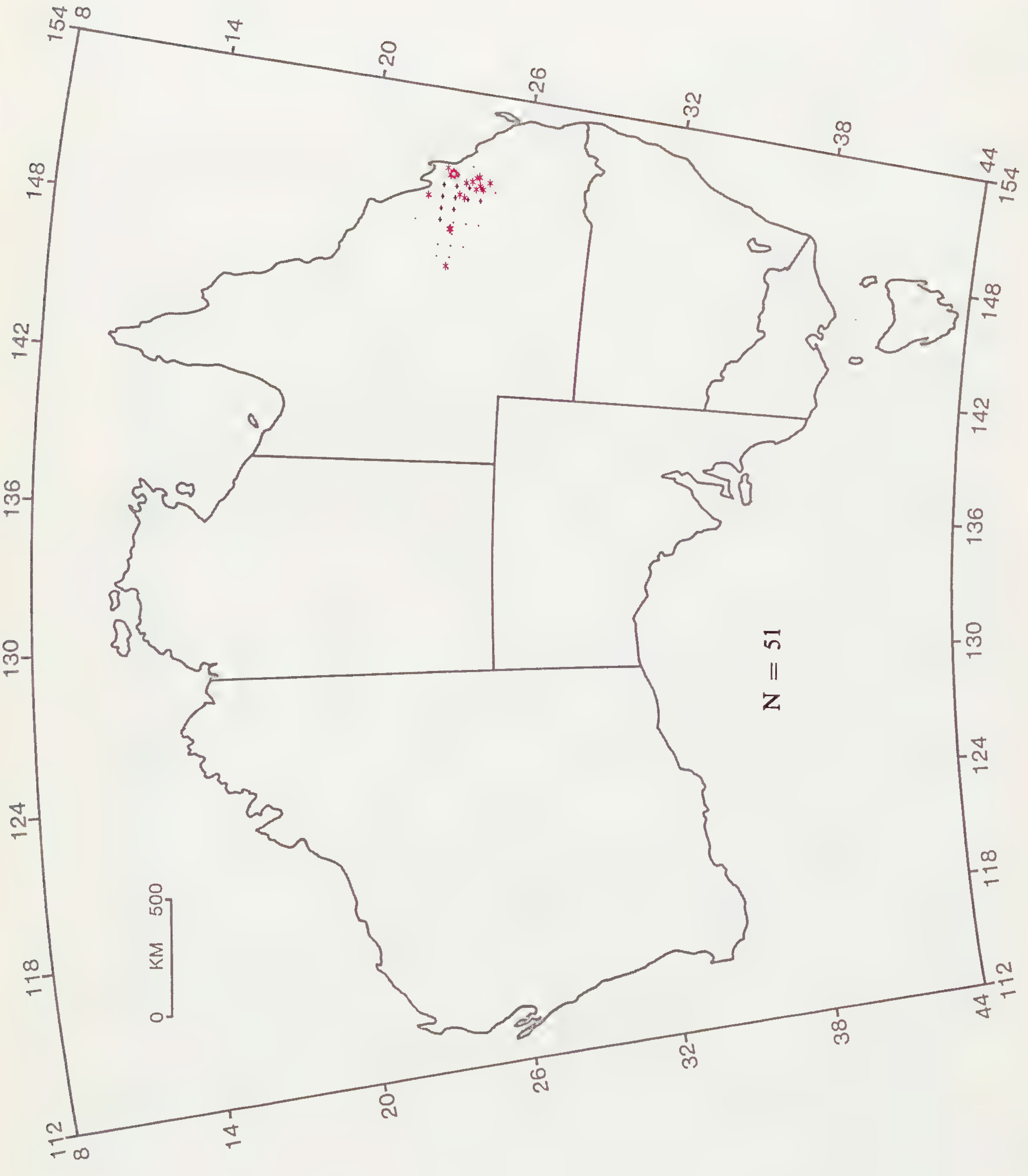

N = 128
0 KM 500
112
118
124
130
136
142
148
154
8
14
20
26
32
38
44

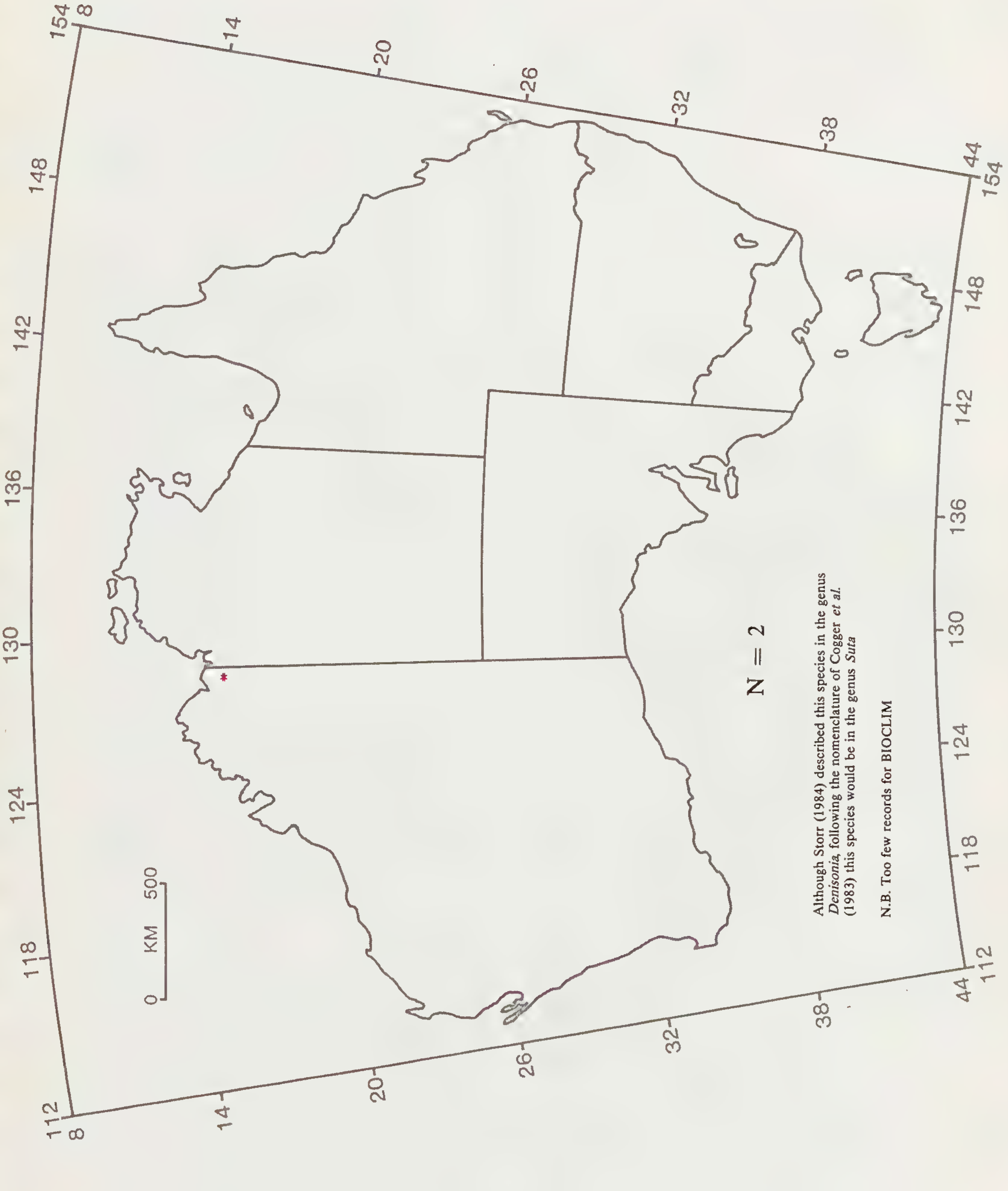
Map 16 Denisonia devisi




N = 117
0 KM 500
112
118
124
130
136
142
148
154
8
14
20
26
32
38
44

Map 18 Denisonia maculata

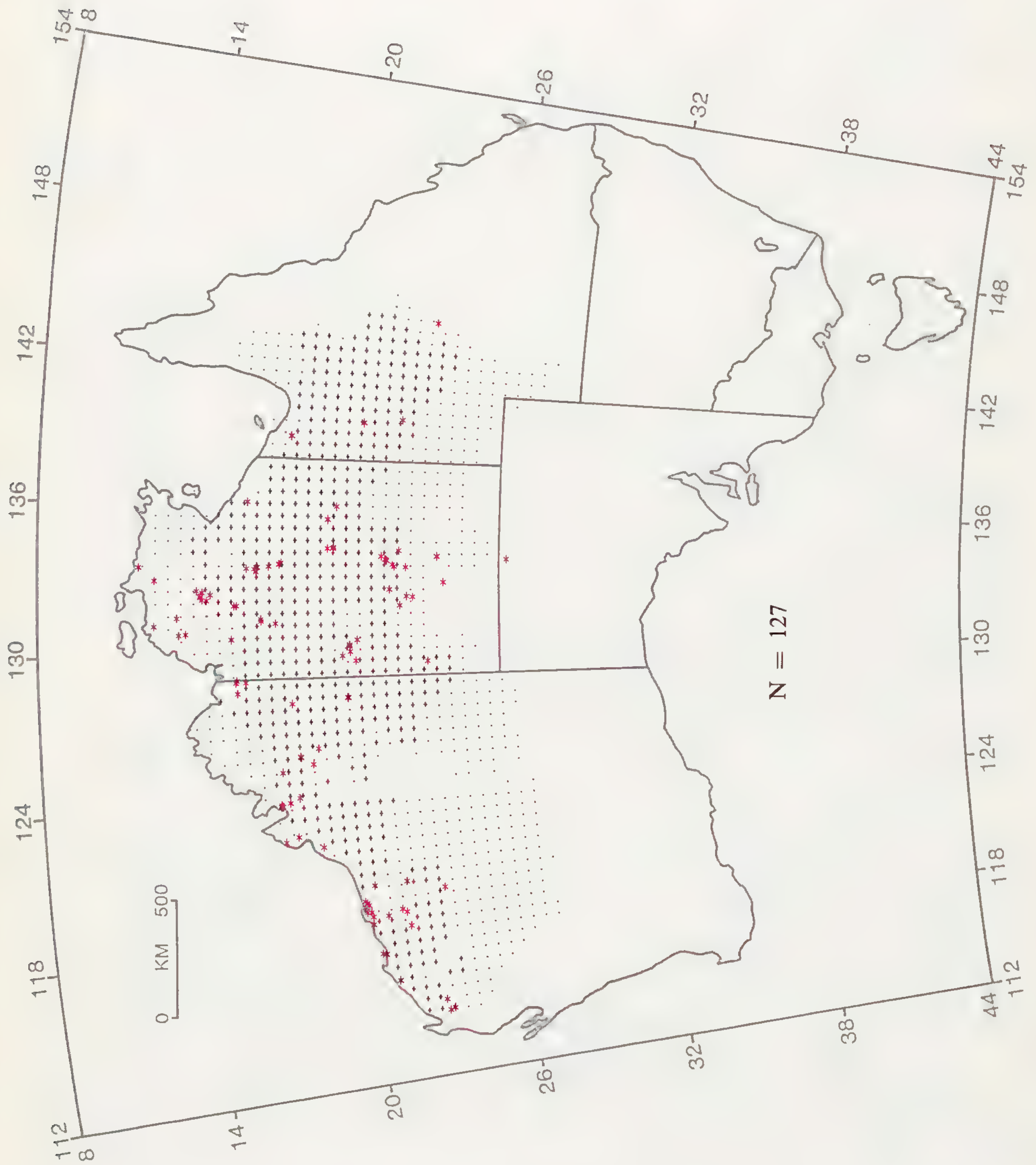


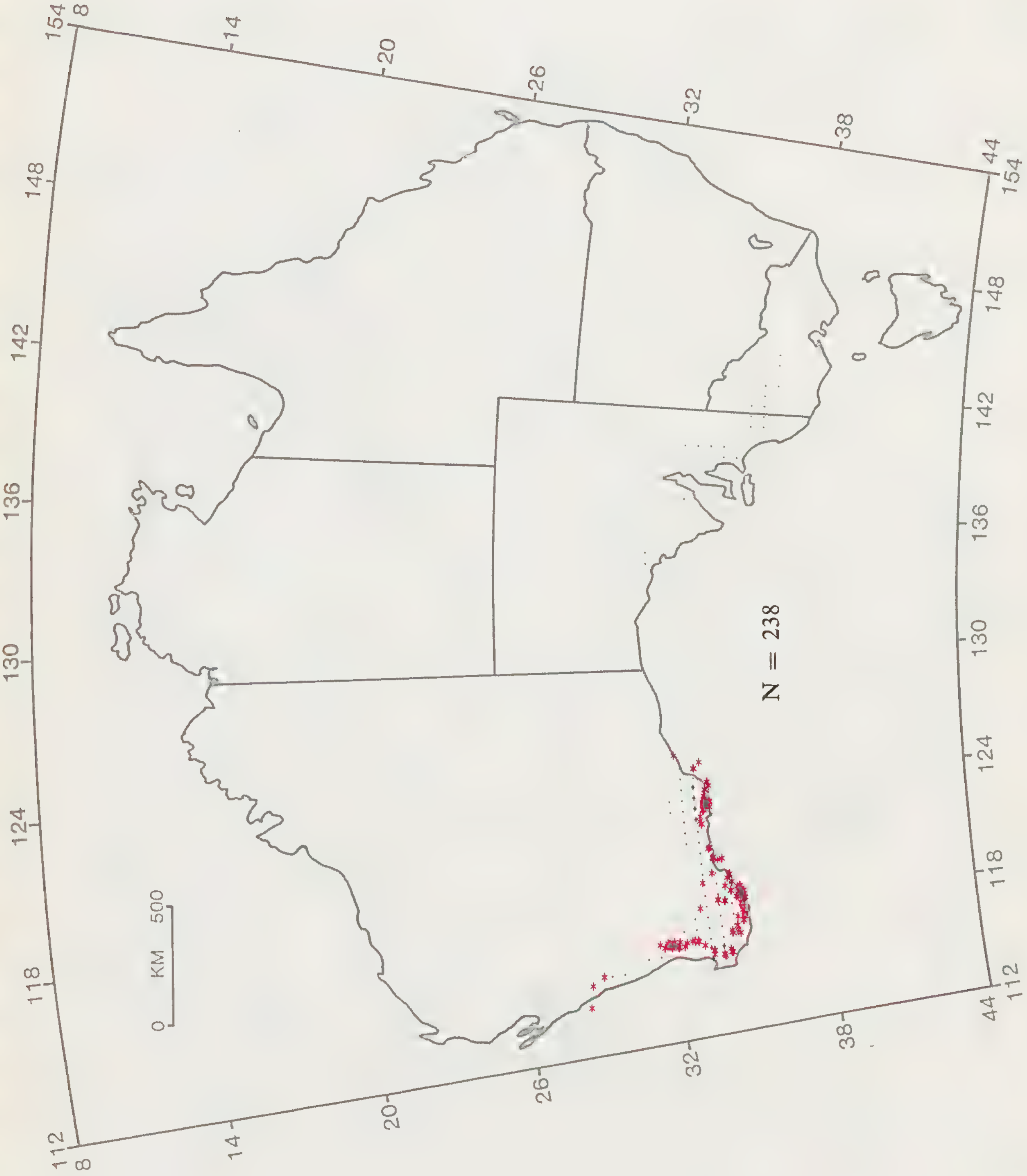


Although Storr (1984) described this species in the genus *Denisonia*, following the nomenclature of Cogger *et al.* (1983) this species would be in the genus *Suta*

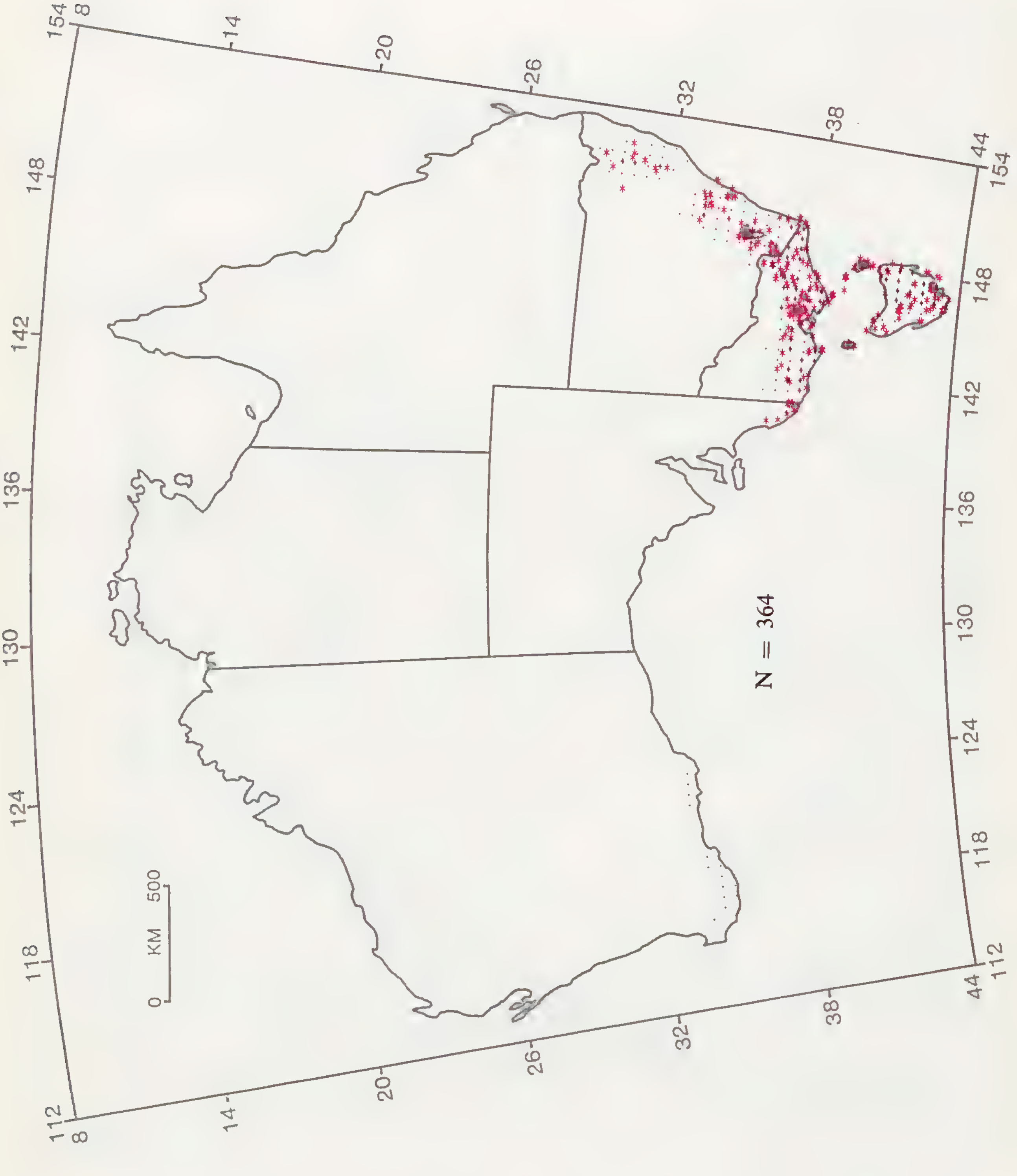
N.B. Too few records for BIOCLIM

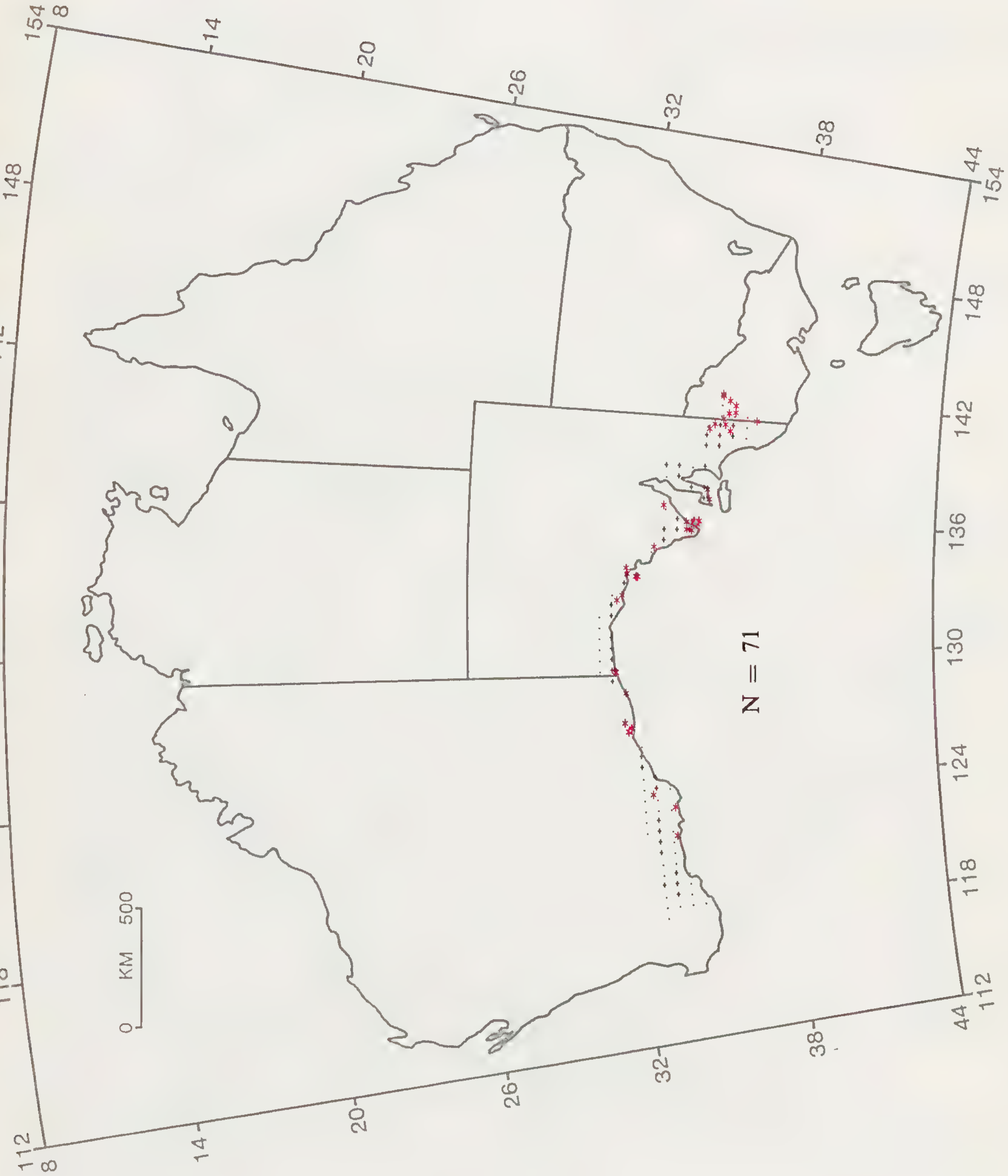
Map 20 Denisonia punctata



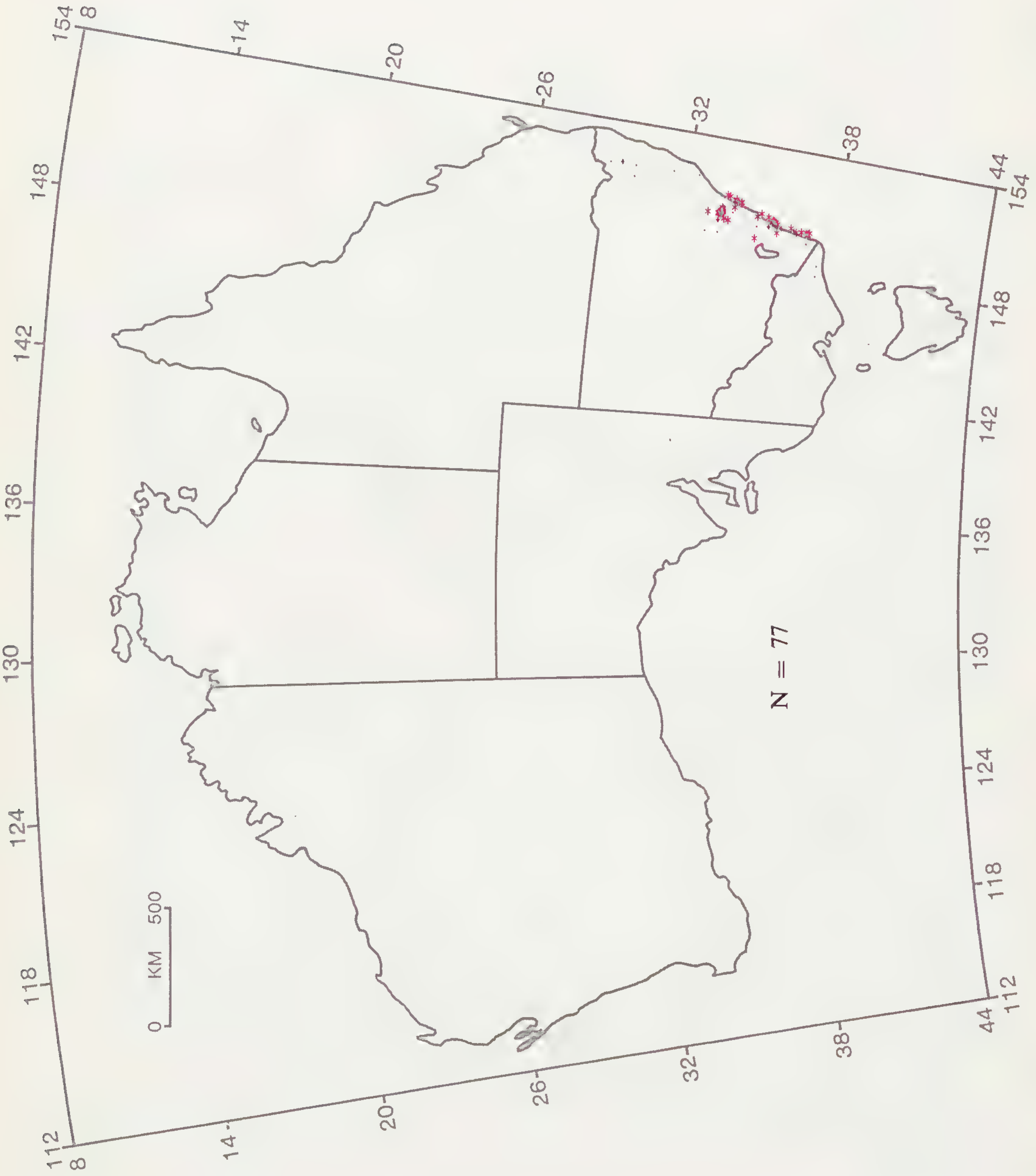

N = 238
0 KM 500
112
118
124
130
136
142
148
154
8
14
20
26
32
38
44

Map 22 Drysdalia coronoides

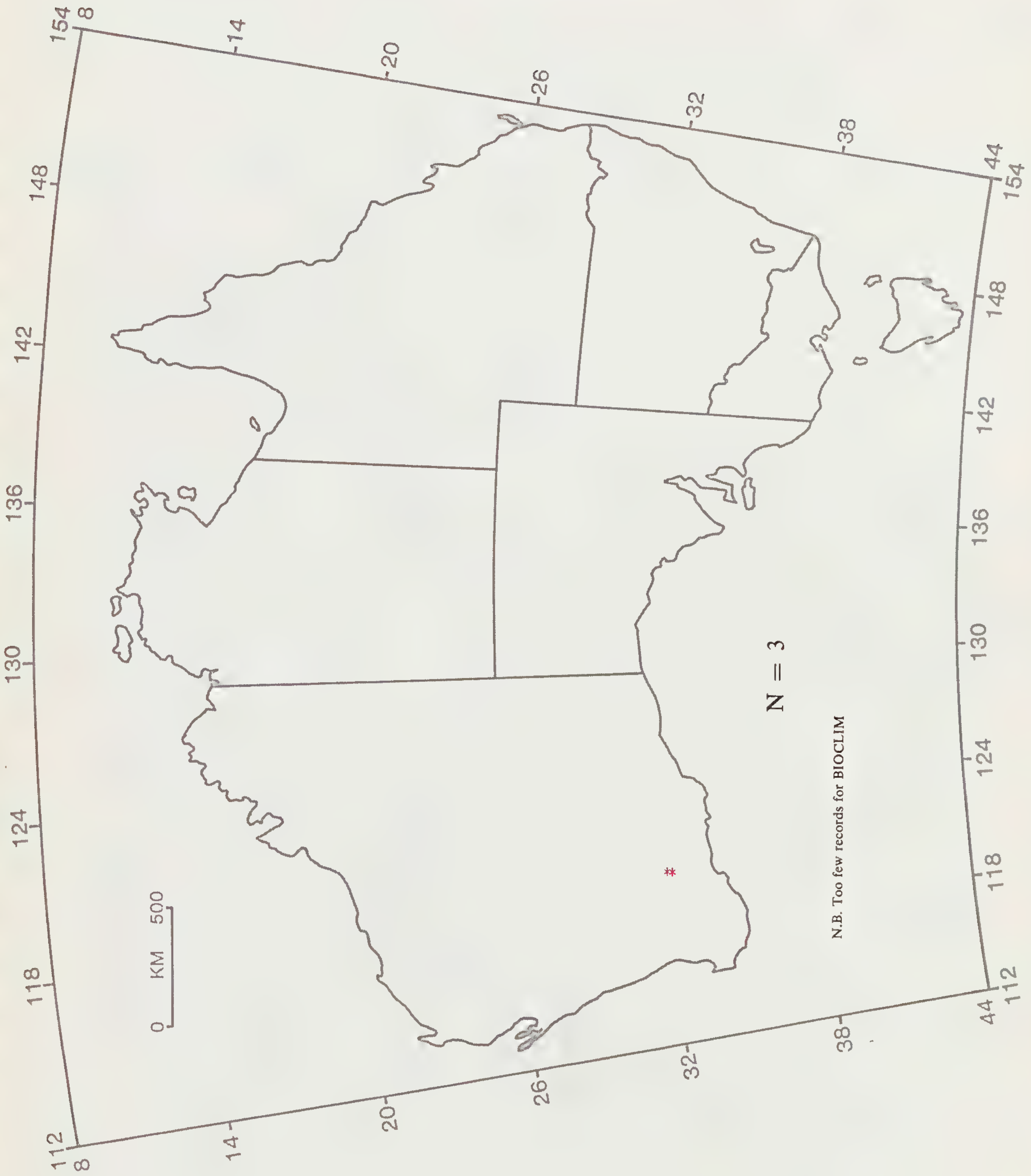



8
14
20
26
32
38
44
112
118
124
130
136
142
148
154
0 KM 500
N = 71

Map 24 Drysdalia rhodogaster



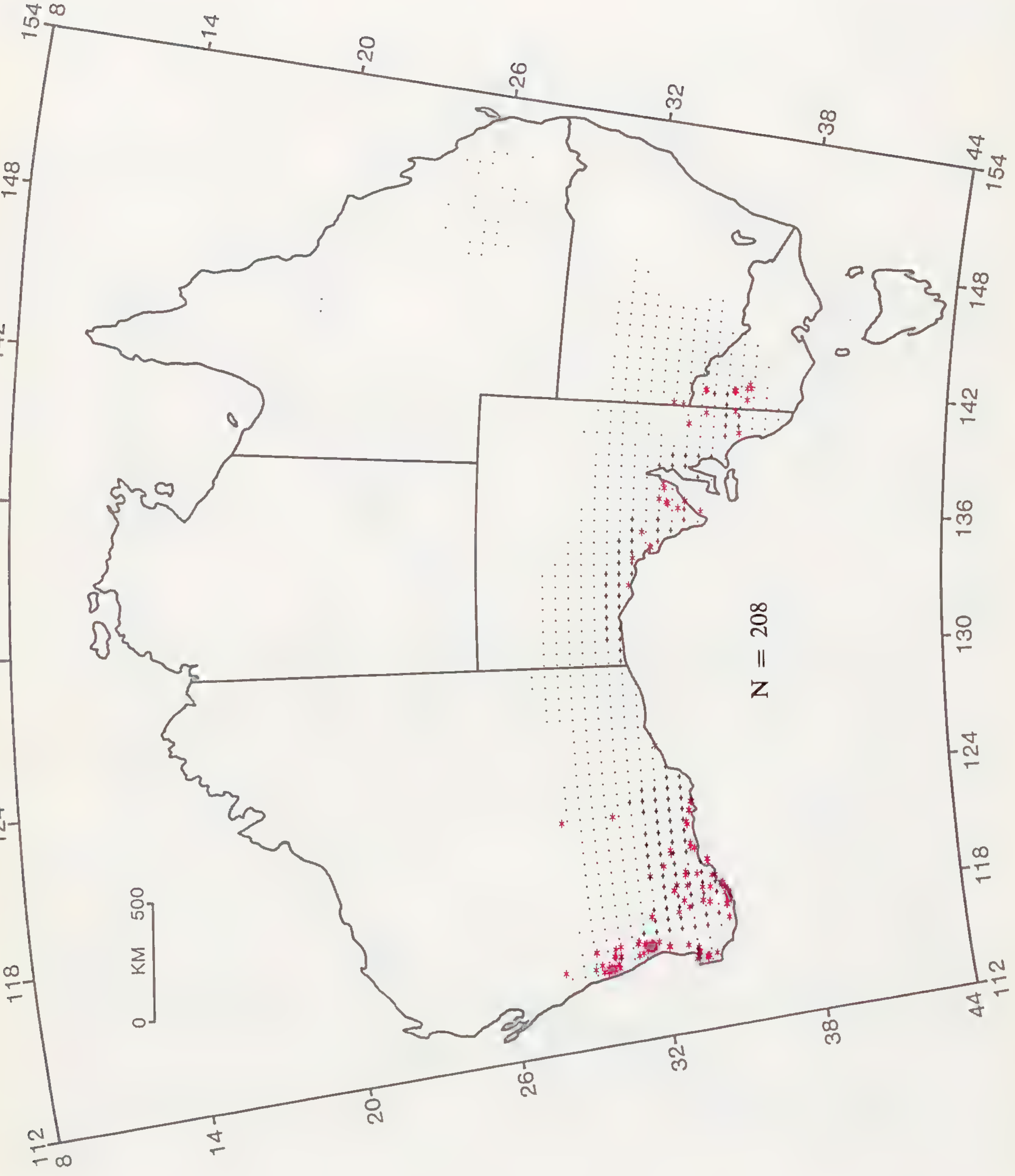
Echiopsis atriceps **Map 25**

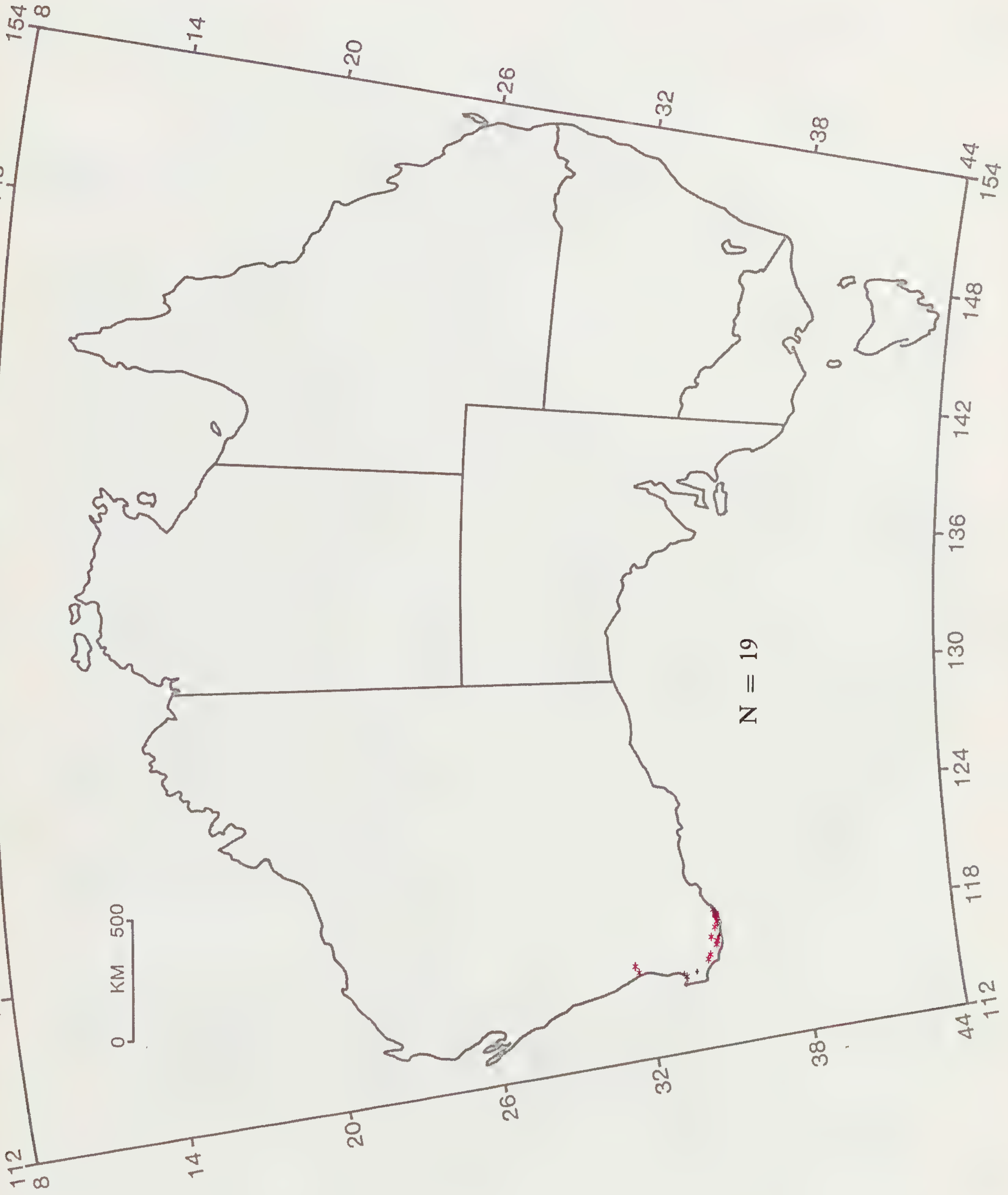


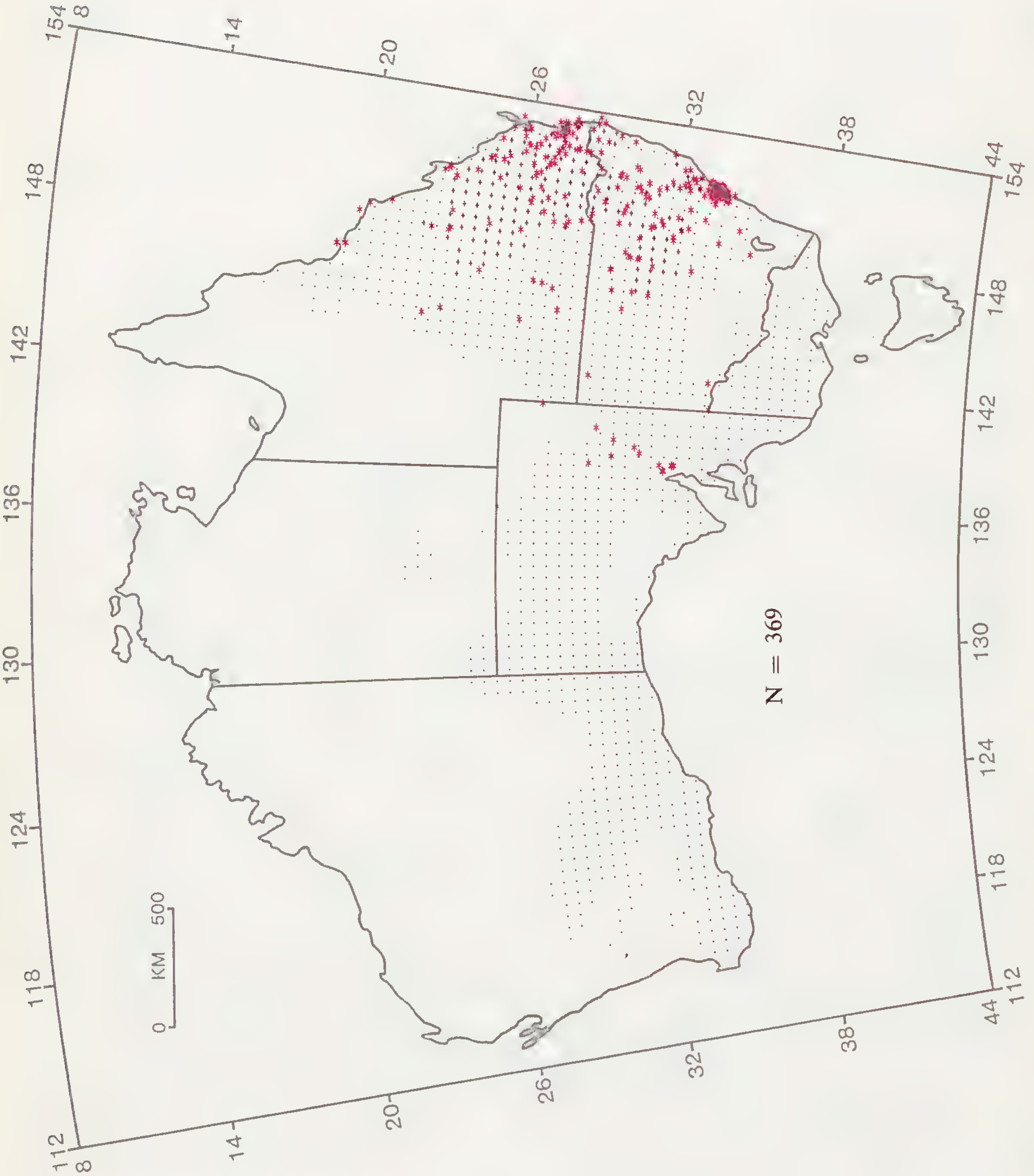
N = 3

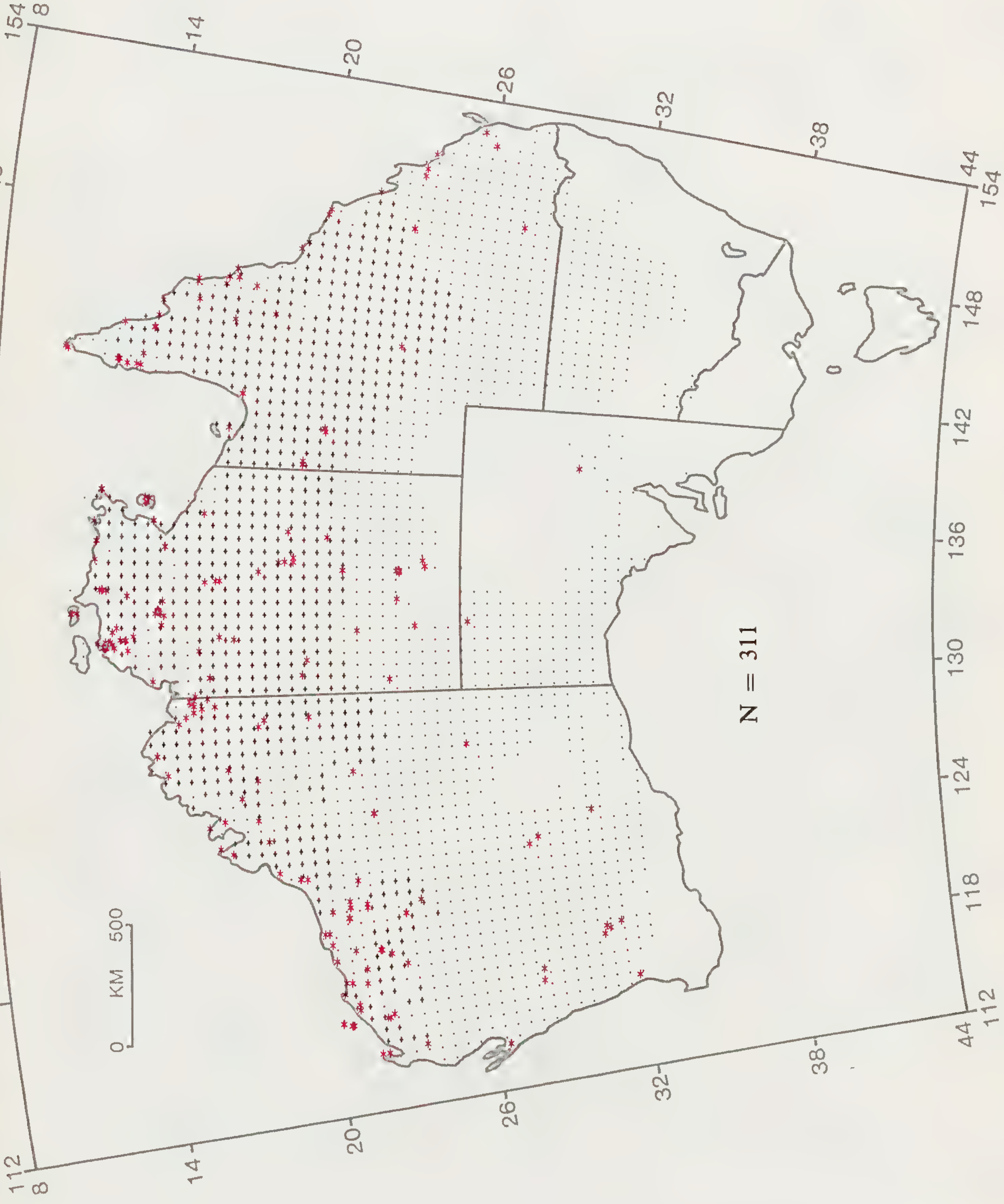
N.B. Too few records for BIOCLIM

Map 26 Echiopsis curta

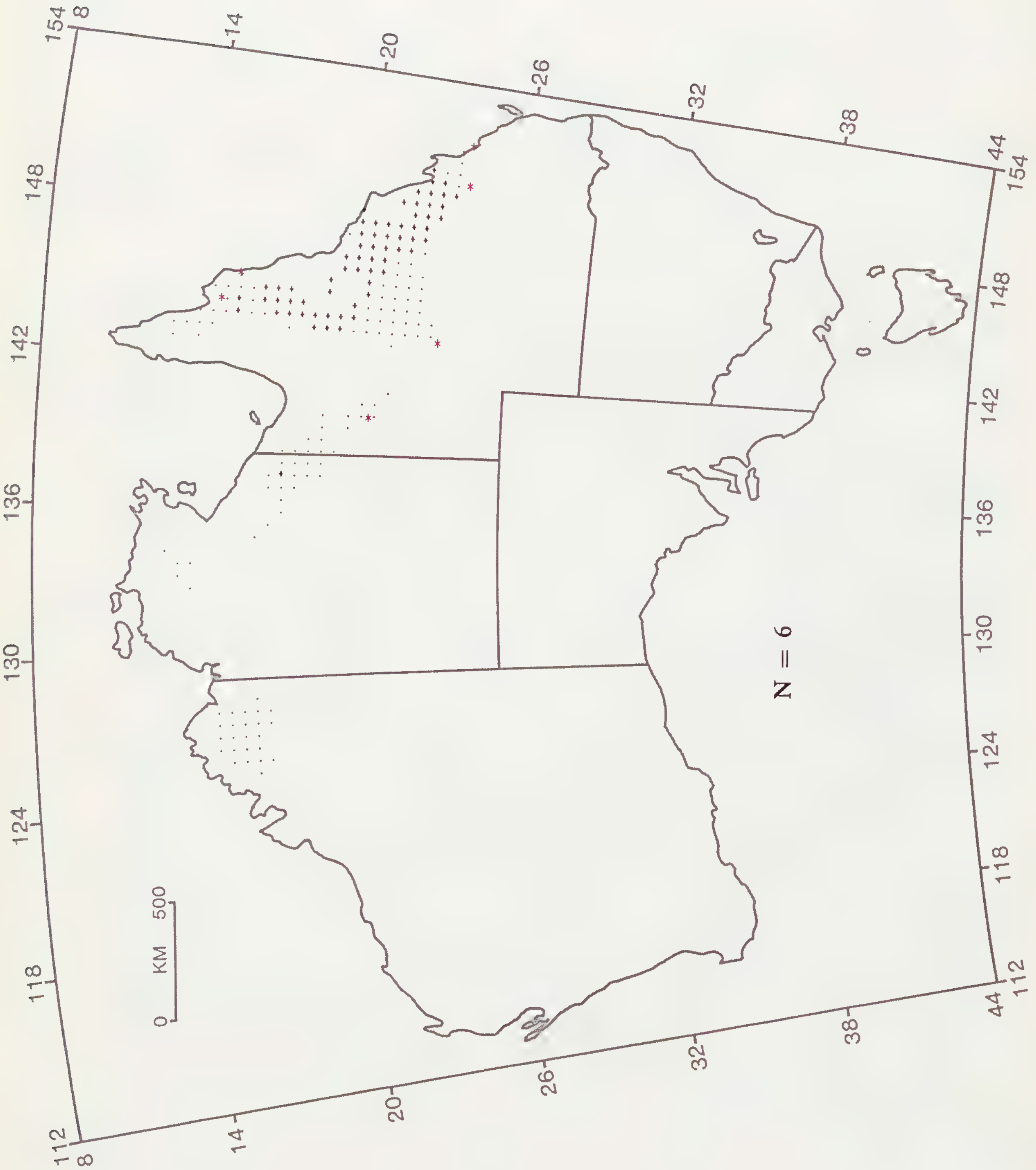


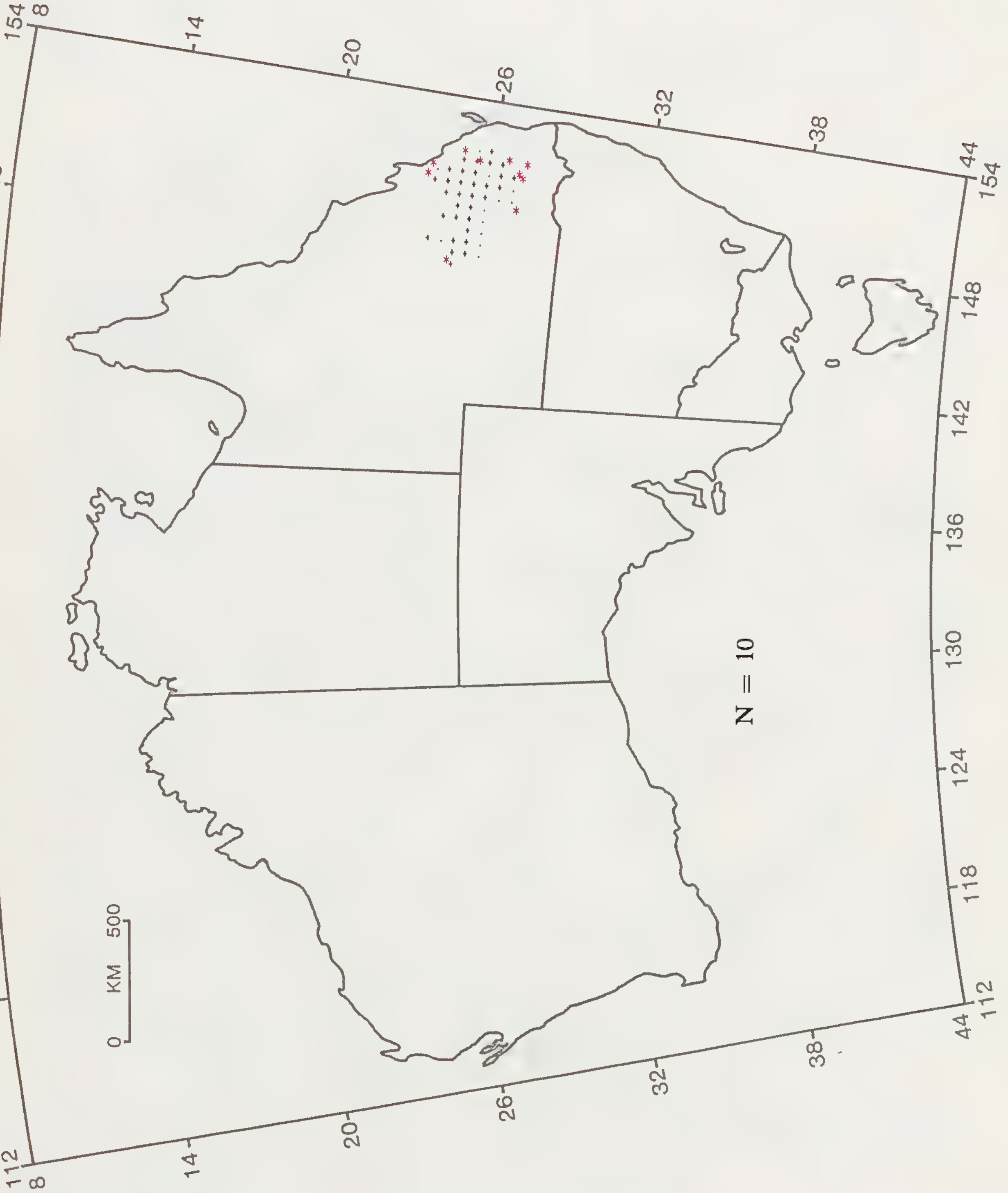

154
8
14
20
26
32
38
44
154
148
142
136
130
124
118
112
112
8
14
20
26
32
38
44
112
118
124
130
136
142
148
0 KM 500
N = 19


154
8
14
20
26
32
38
44
154
148
142
136
130
124
118
112
8
14
20
26
32
38
44
112
118
124
130
136
142
148
N = 369
0 KM 500

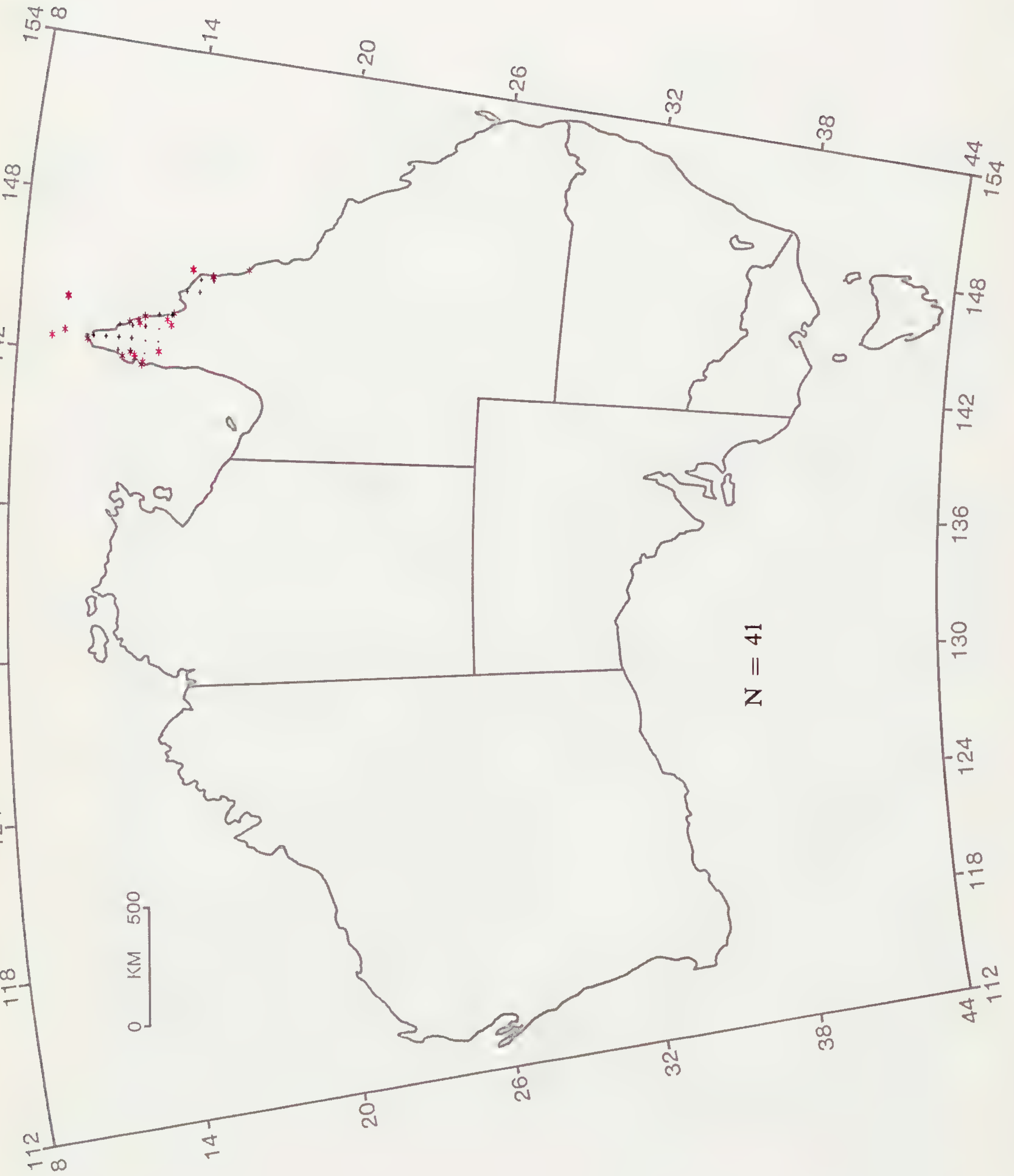

N = 311
0 KM 500
8
14
20
26
32
38
44
112
118
124
130
136
142
148
154

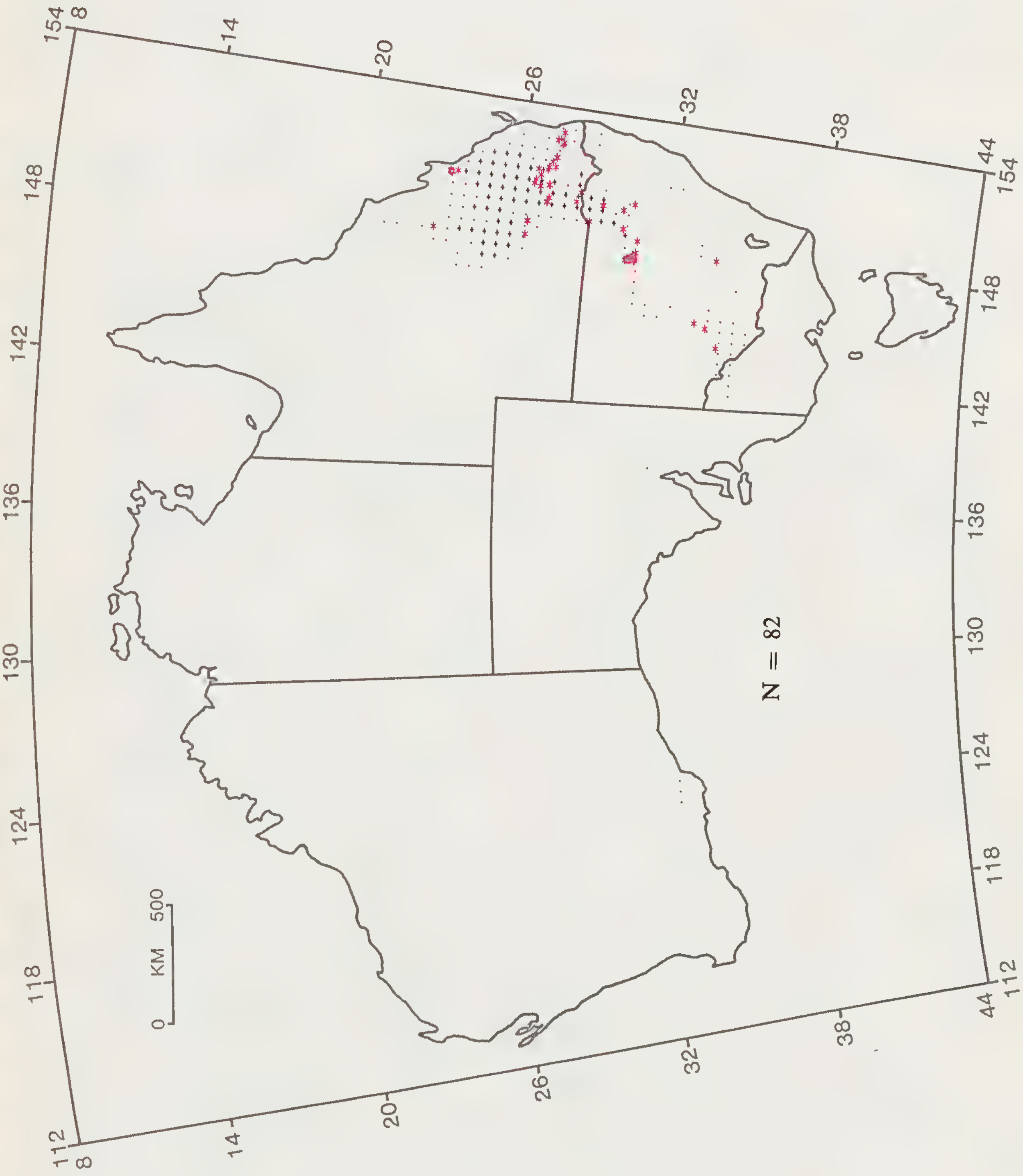
Map 30 Glyphodon barnardi



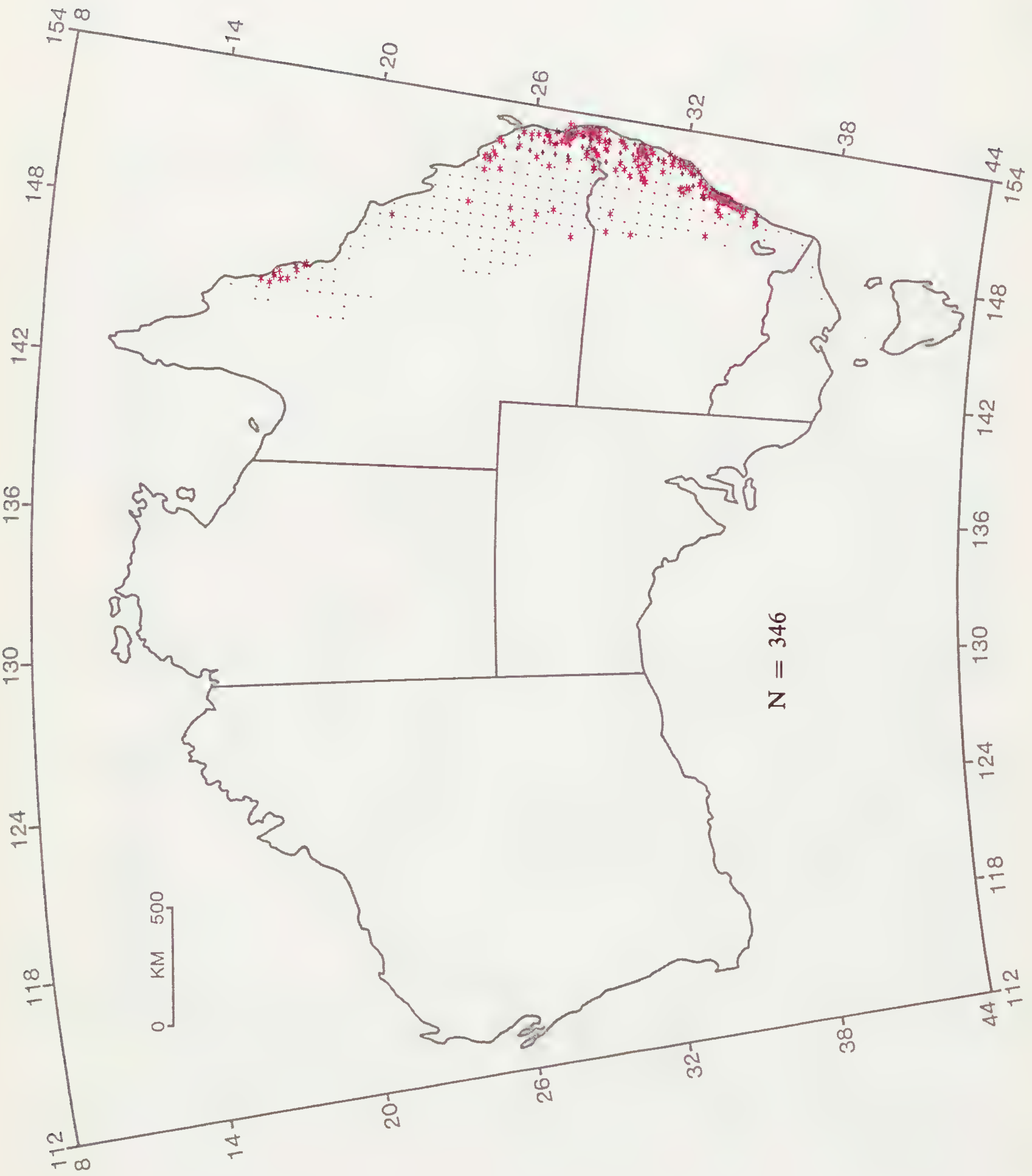

112
118
124
130
136
142
148
154
8
14
20
26
32
38
44
0 KM 500
N = 10

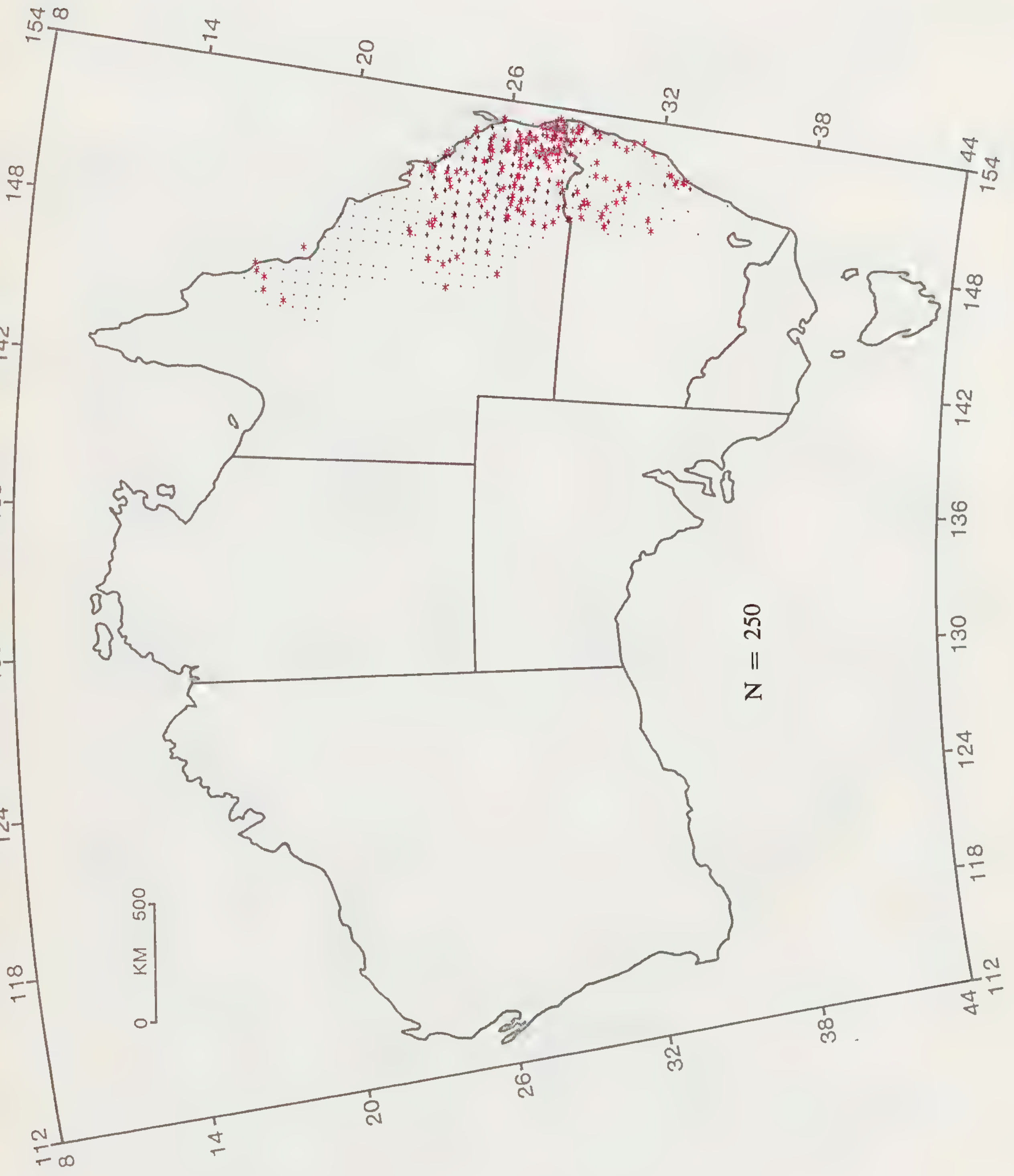
Map 32 Glyphodon tristis



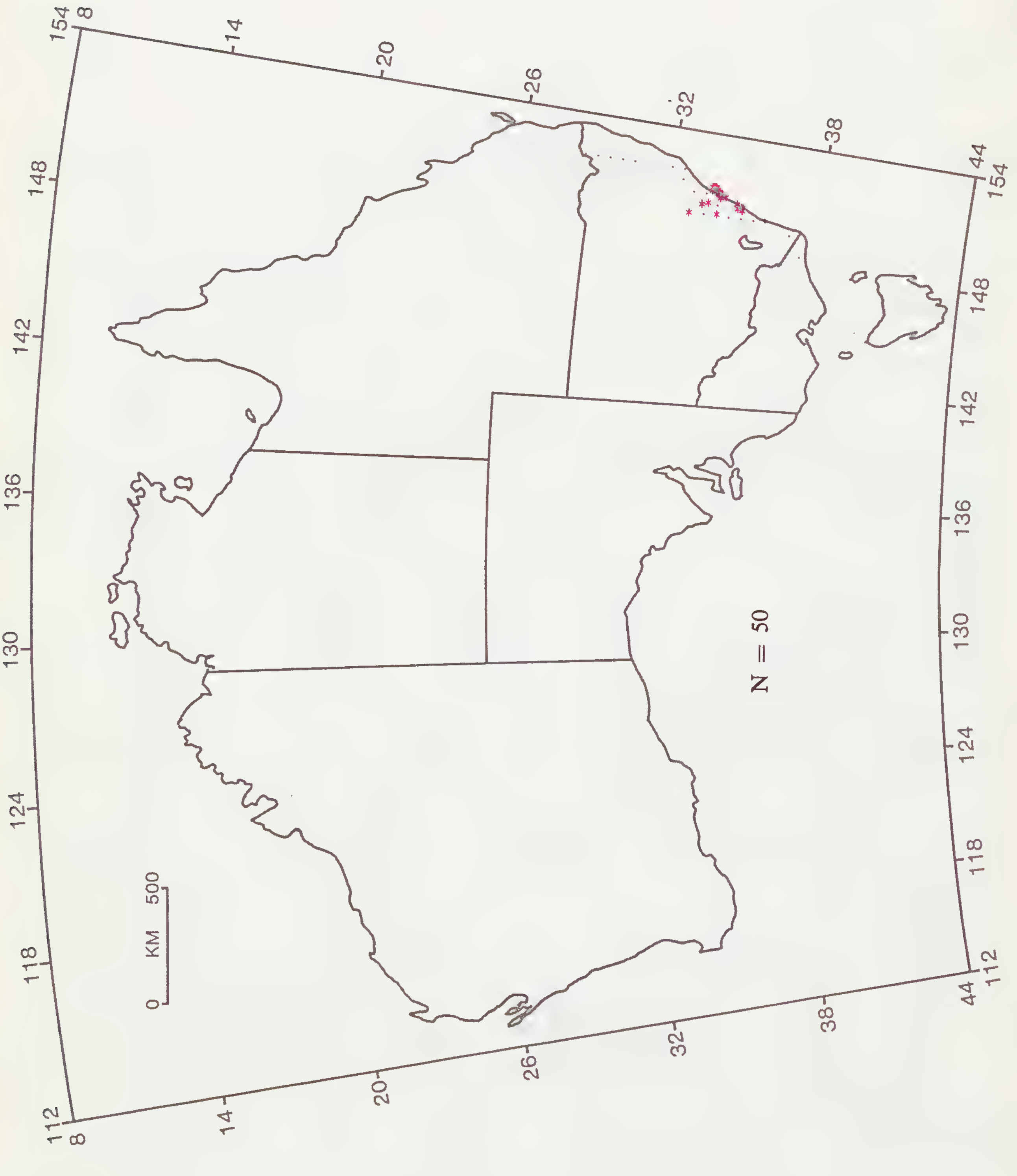

N = 82
0 KM 500
154
8
14
20
26
32
38
44
154
148
142
136
130
124
118
112
44
112
38
32
26
20
14
8
112
118
124
130
136
142
148

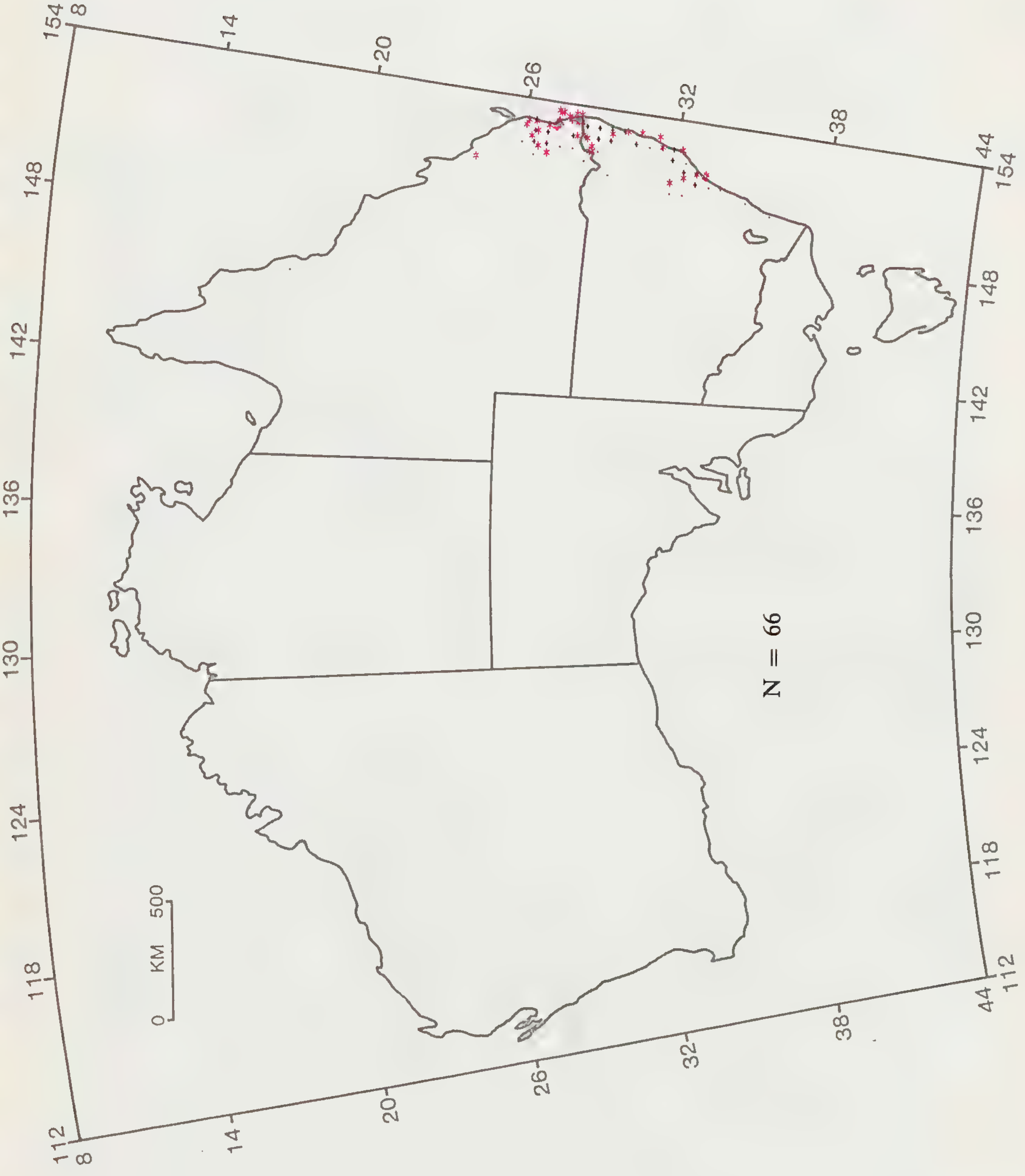
Map 34 Hemiaspis signata



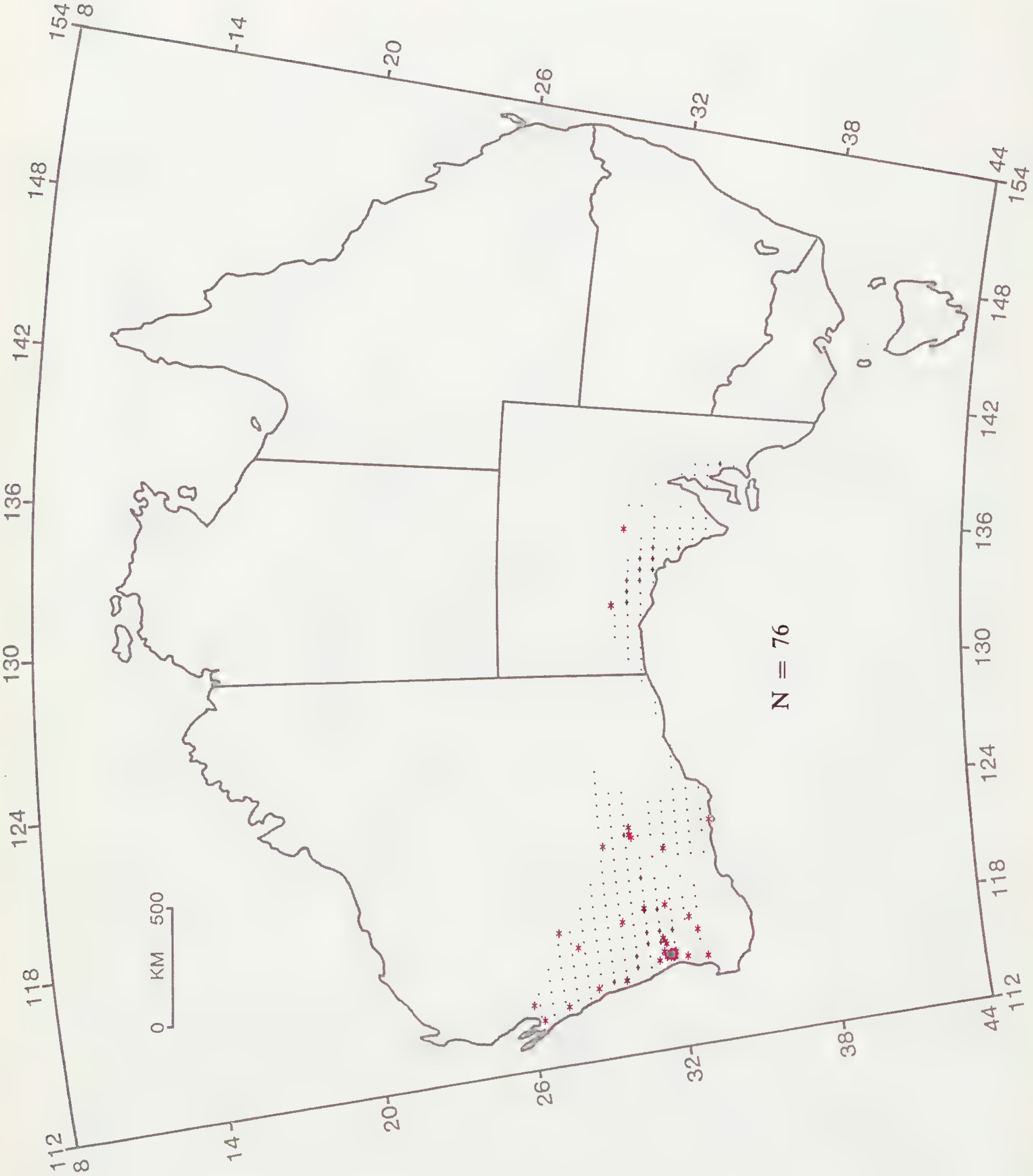

154
8
14
20
26
32
38
44
154
148
142
136
130
124
118
112
44
112
8
0
KM
500
N = 250

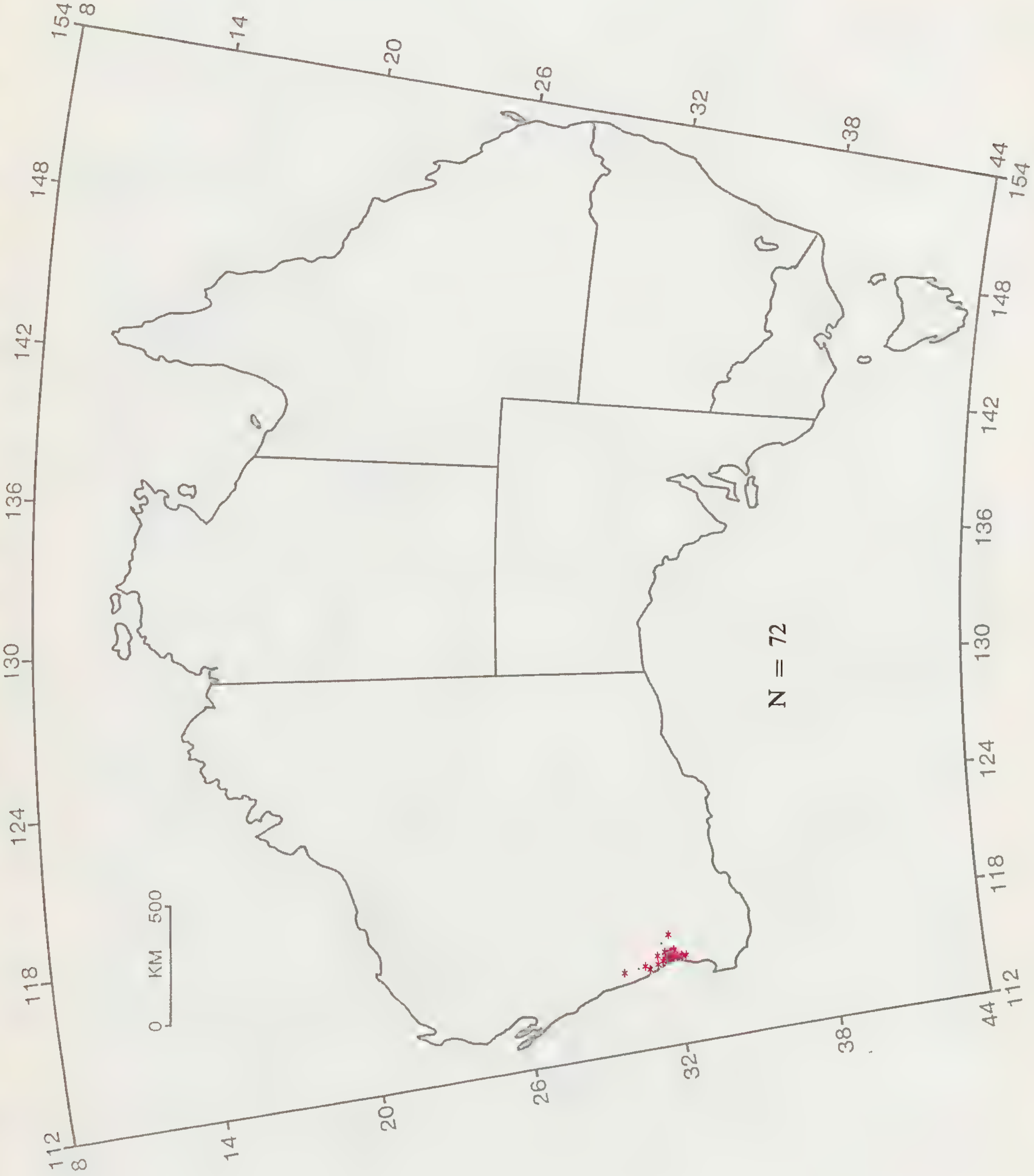
Map 36 Hoplocephalus bungaroides



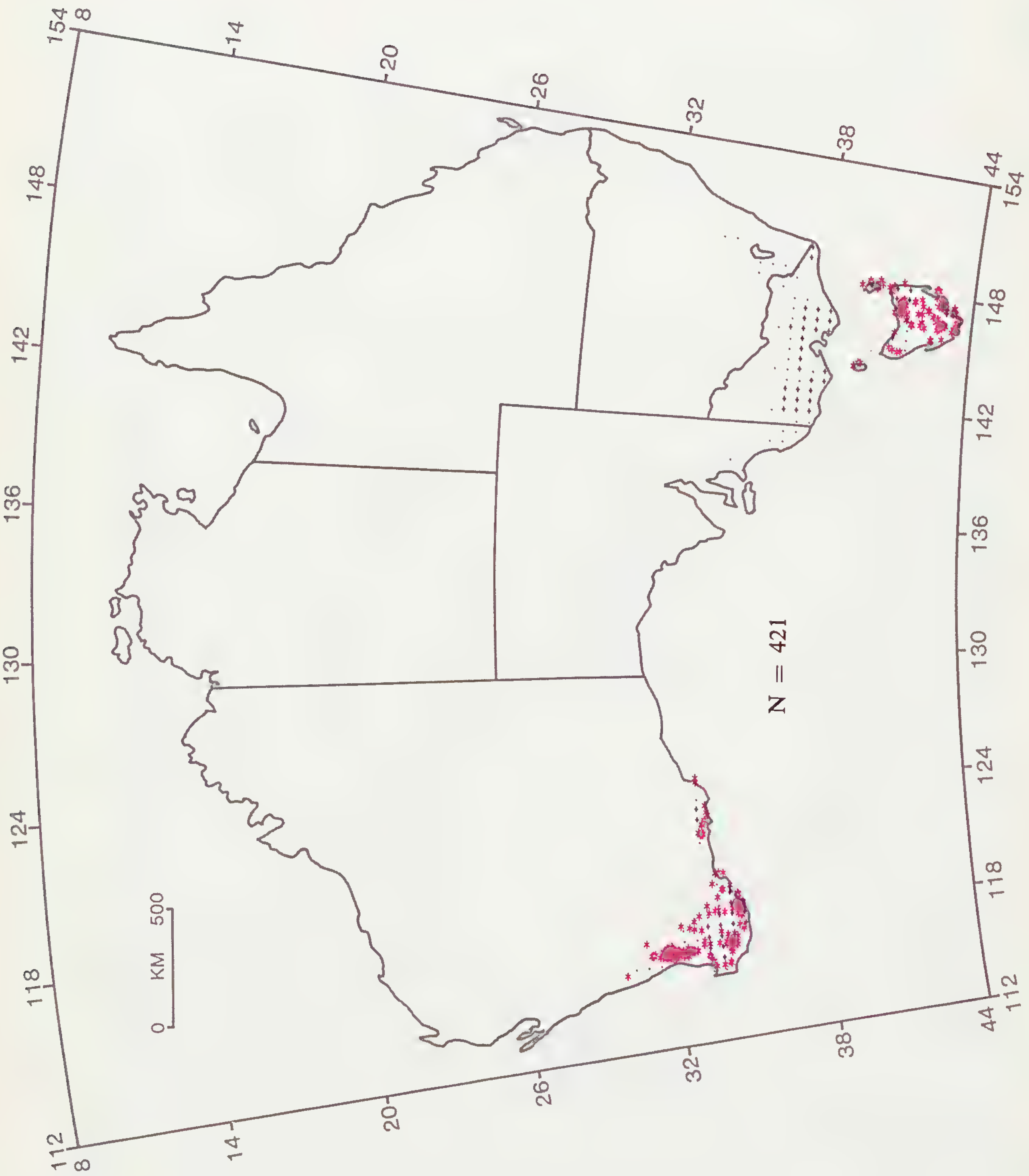

N = 66
0 KM 500
8
14
20
26
32
38
44
112
118
124
130
136
142
148
154

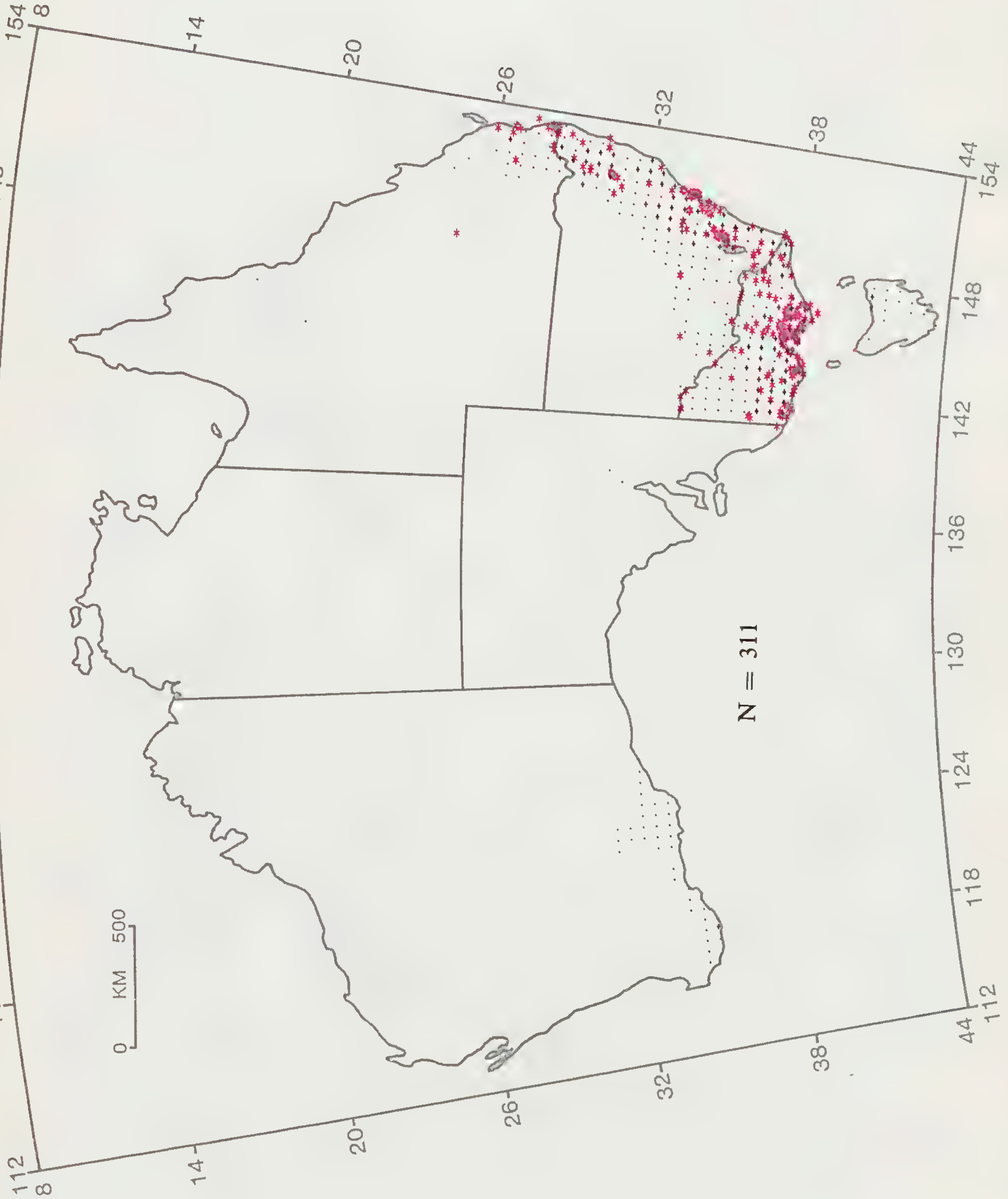
Map 38 Neelaps bimaculatus

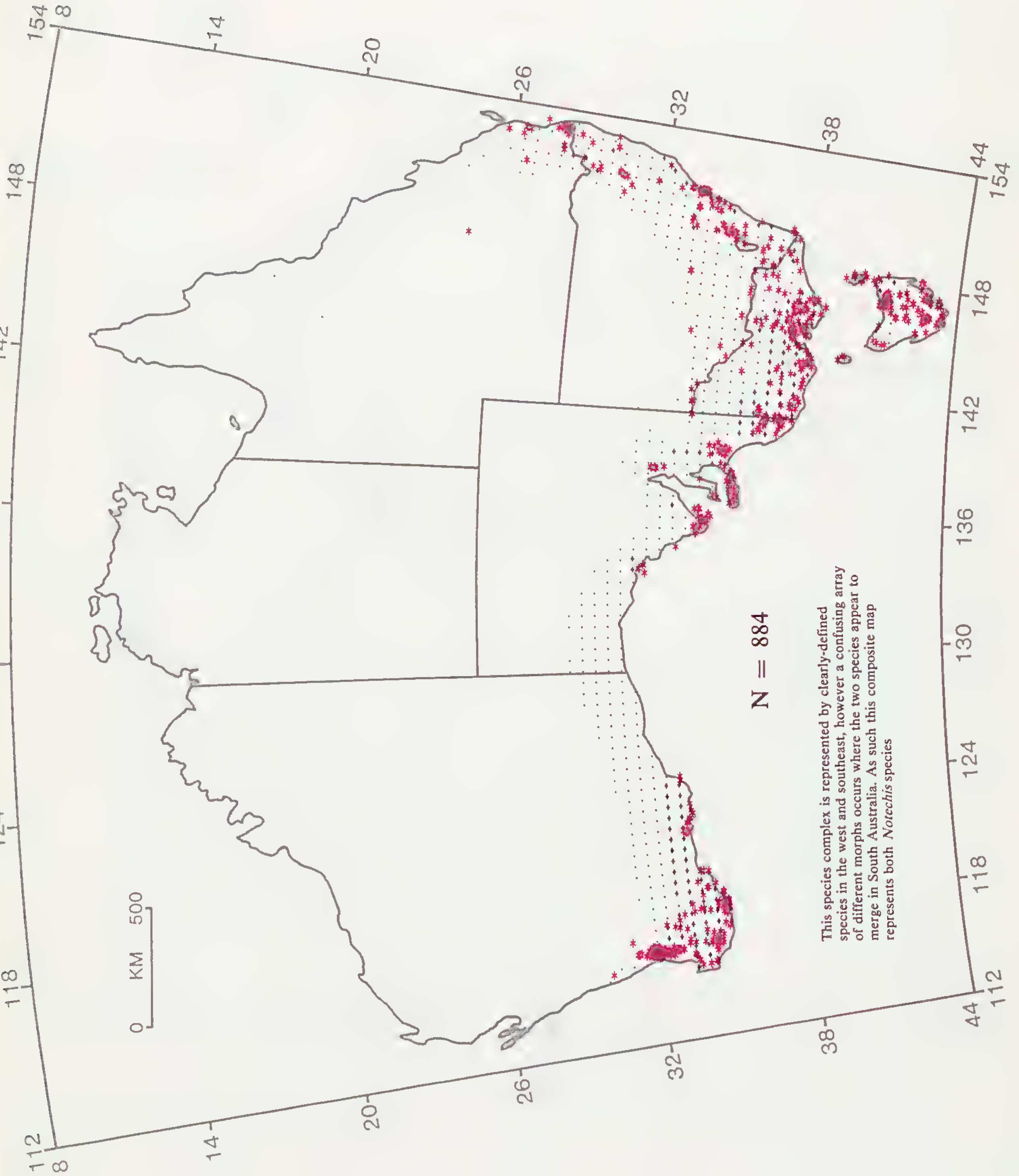



N = 72
0 KM 500
112
118
124
130
136
142
148
154
8
14
20
26
32
38
44

Map 40 Notechis ater

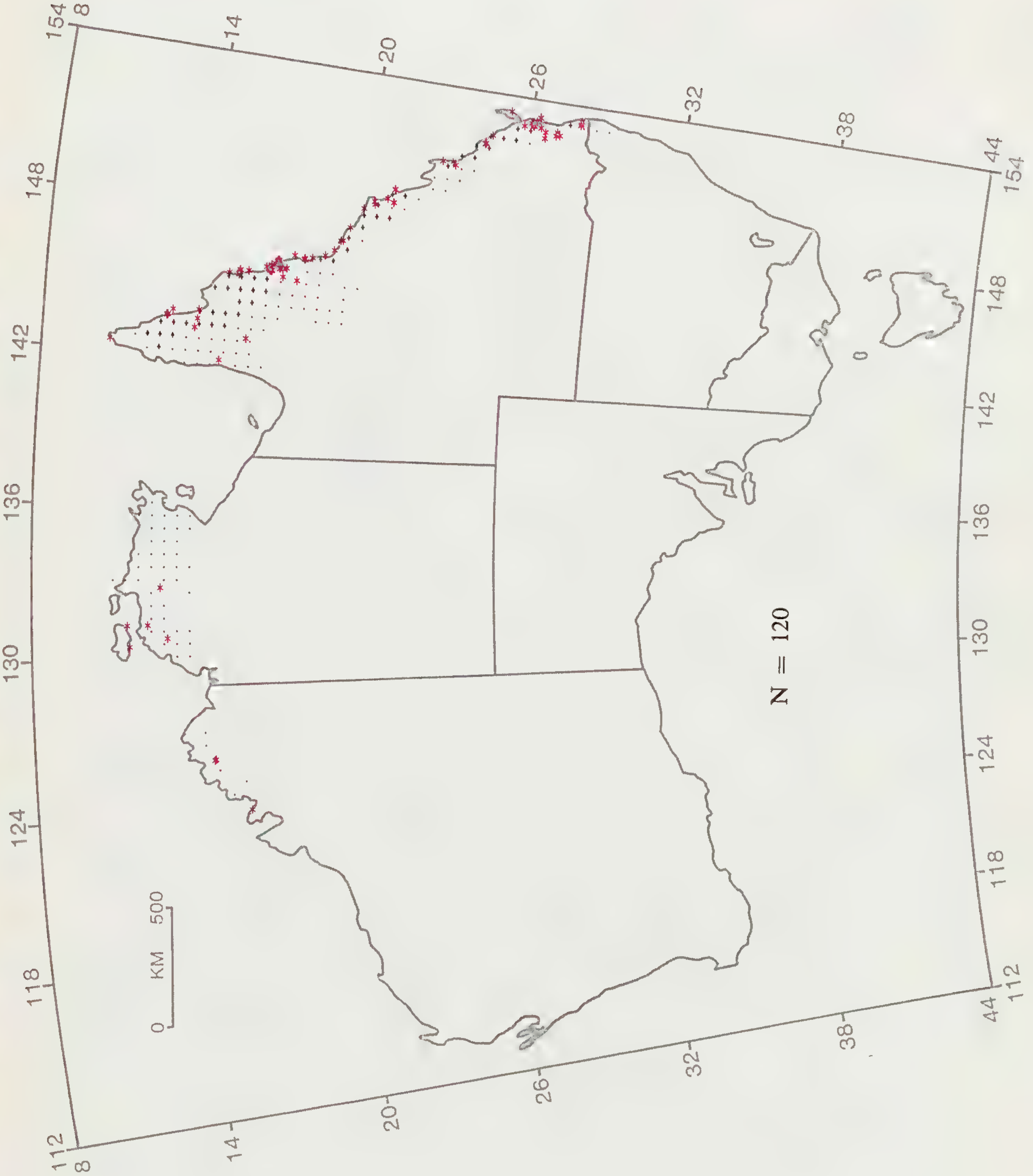



N = 311
0 KM 500
112
118
124
130
136
142
148
154
8
14
20
26
32
38
44

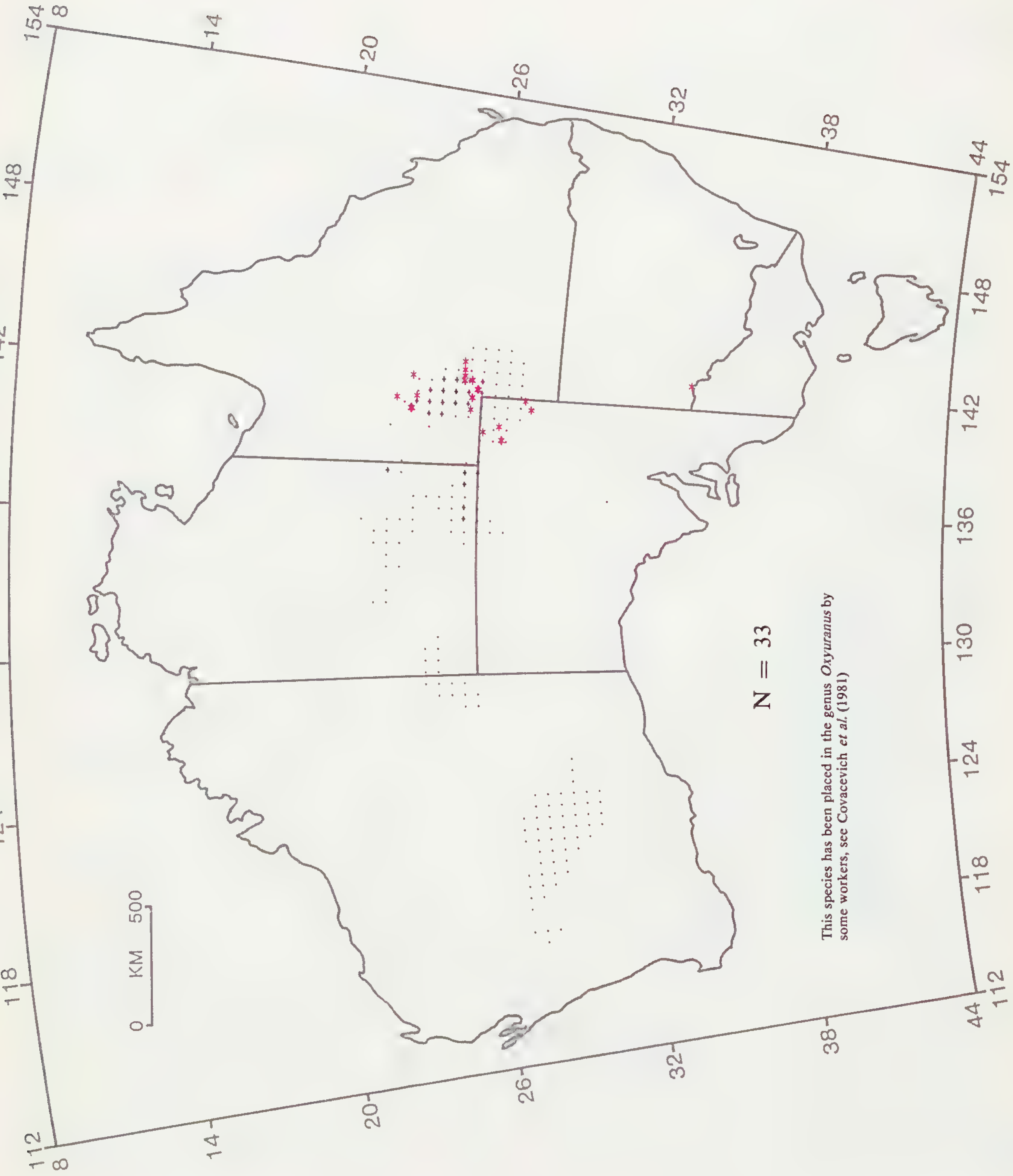


N = 884

This species complex is represented by clearly-defined species in the west and southeast, however a confusing array of different morphs occurs where the two species appear to merge in South Australia. As such this composite map represents both *Notechis* species

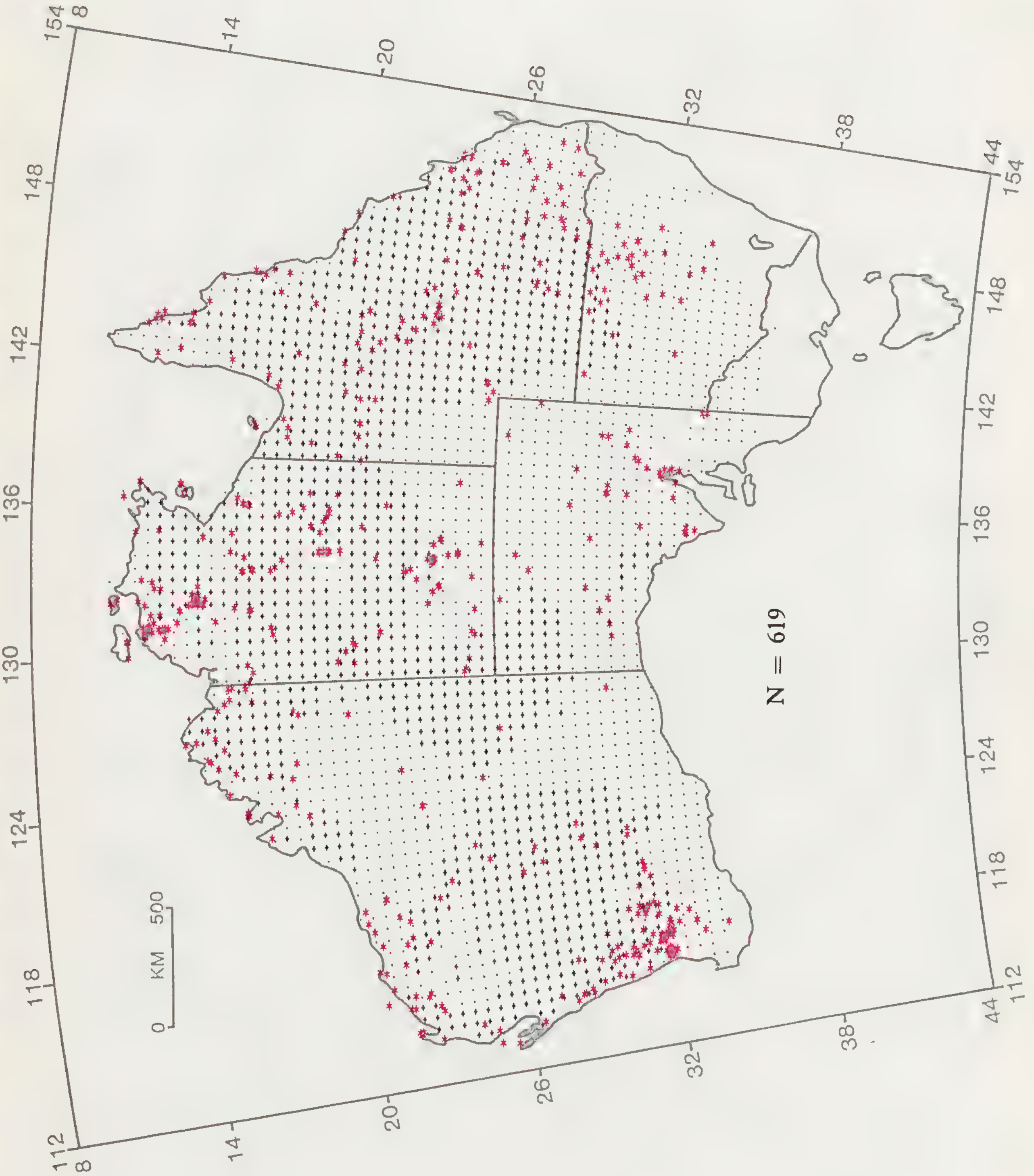

N = 120
0 KM 500
8
14
20
26
32
38
44
112
118
124
130
136
142
148
154

Map 44 Parademansia microlepidota

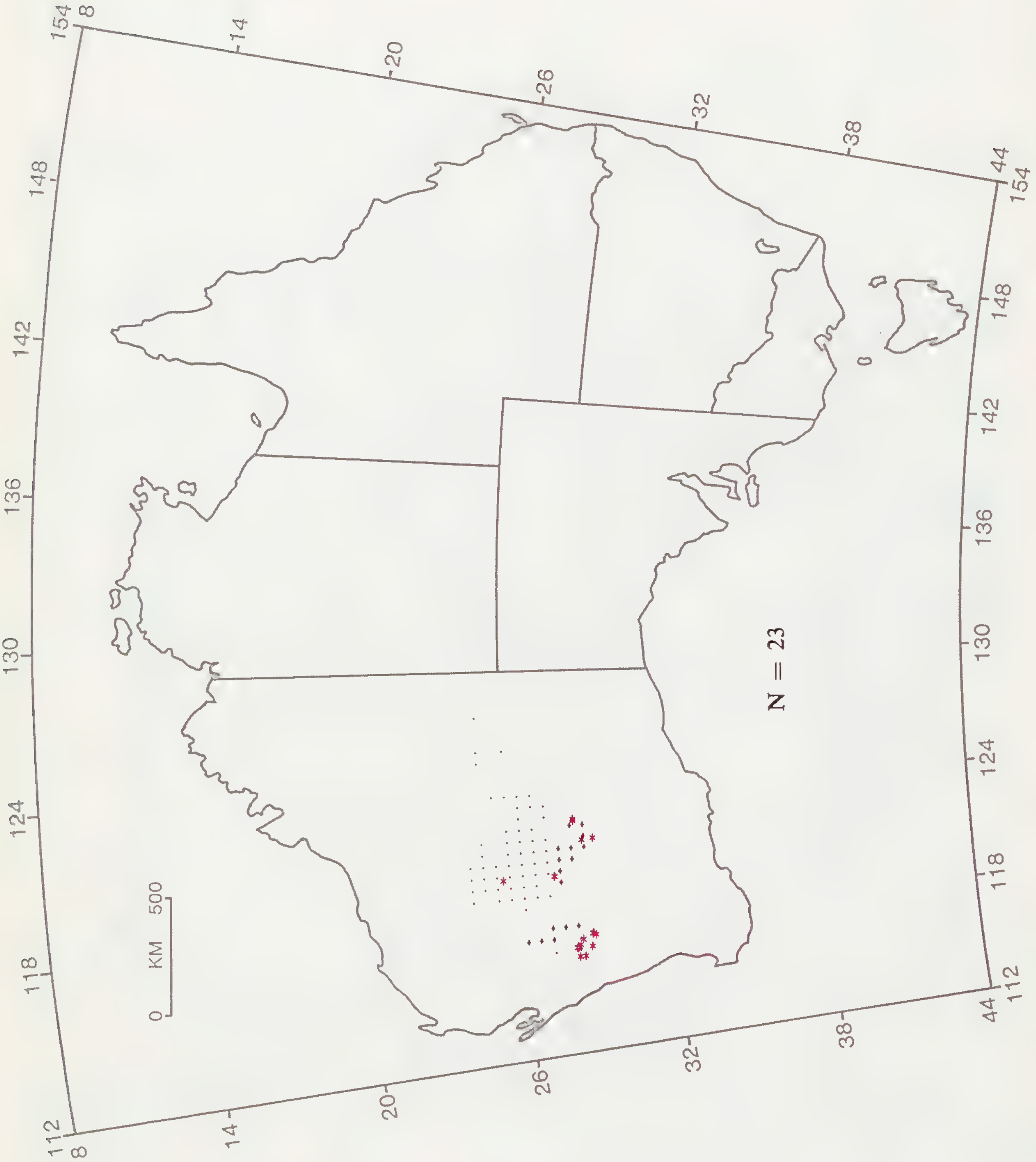


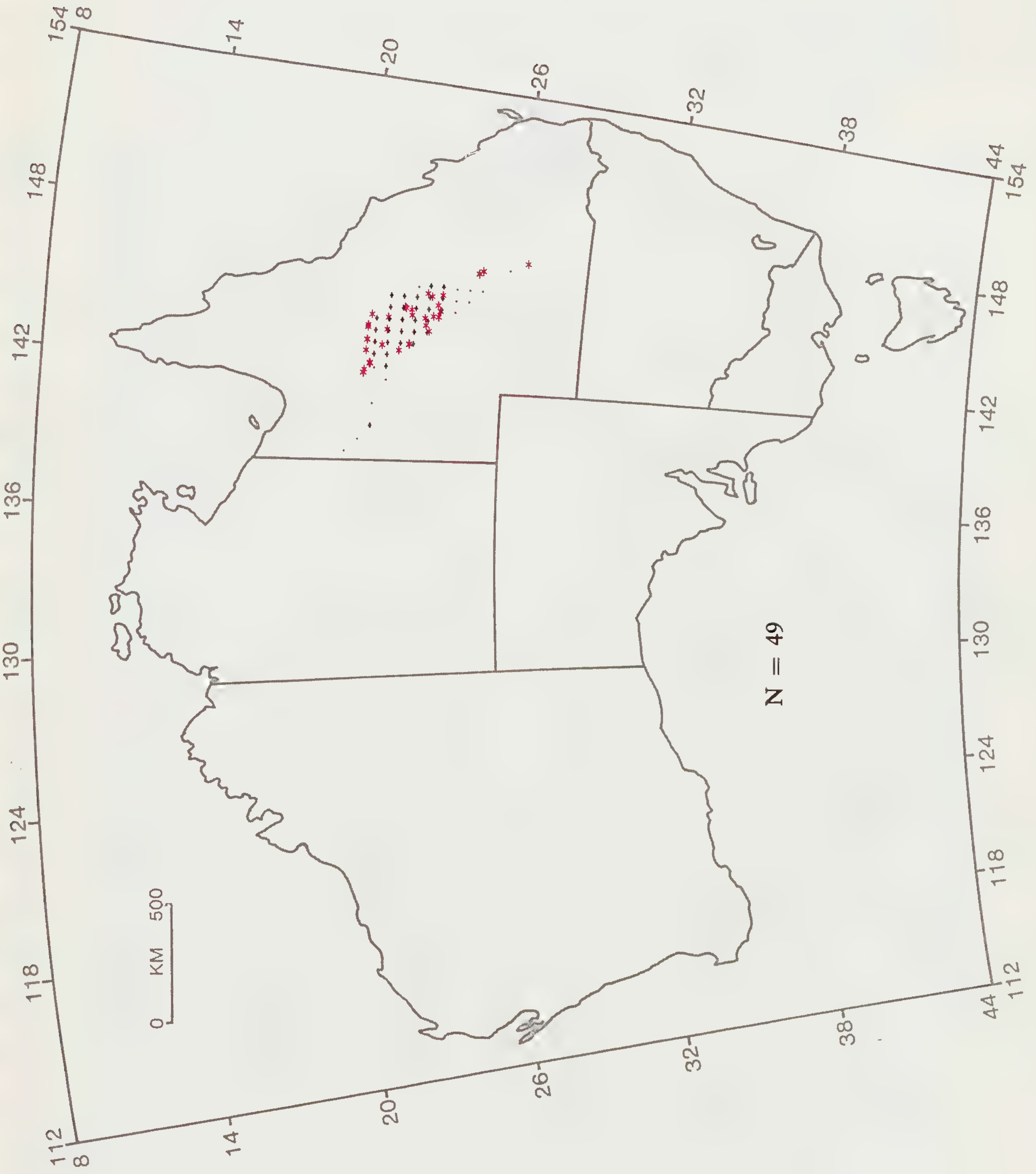
N = 33

This species has been placed in the genus *Oxyuranus* by some workers, see Covacevich *et al.* (1981)

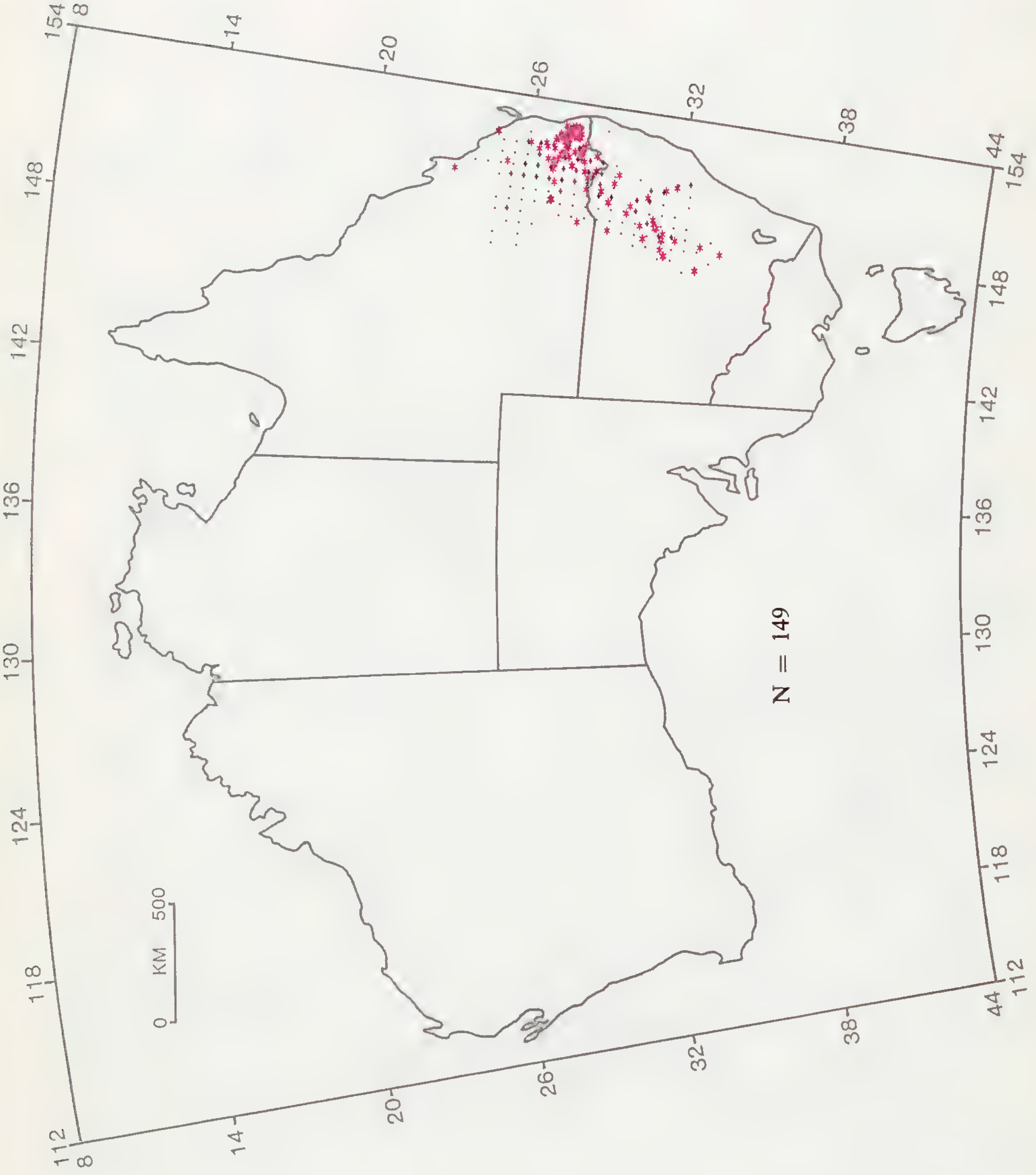

154
8
14
20
26
32
38
44
154
148
142
136
130
124
118
112
44
38
32
26
20
14
8
112
118
124
130
136
142
148
0 KM 500
N = 619

Map 46 Pseudechis butleri

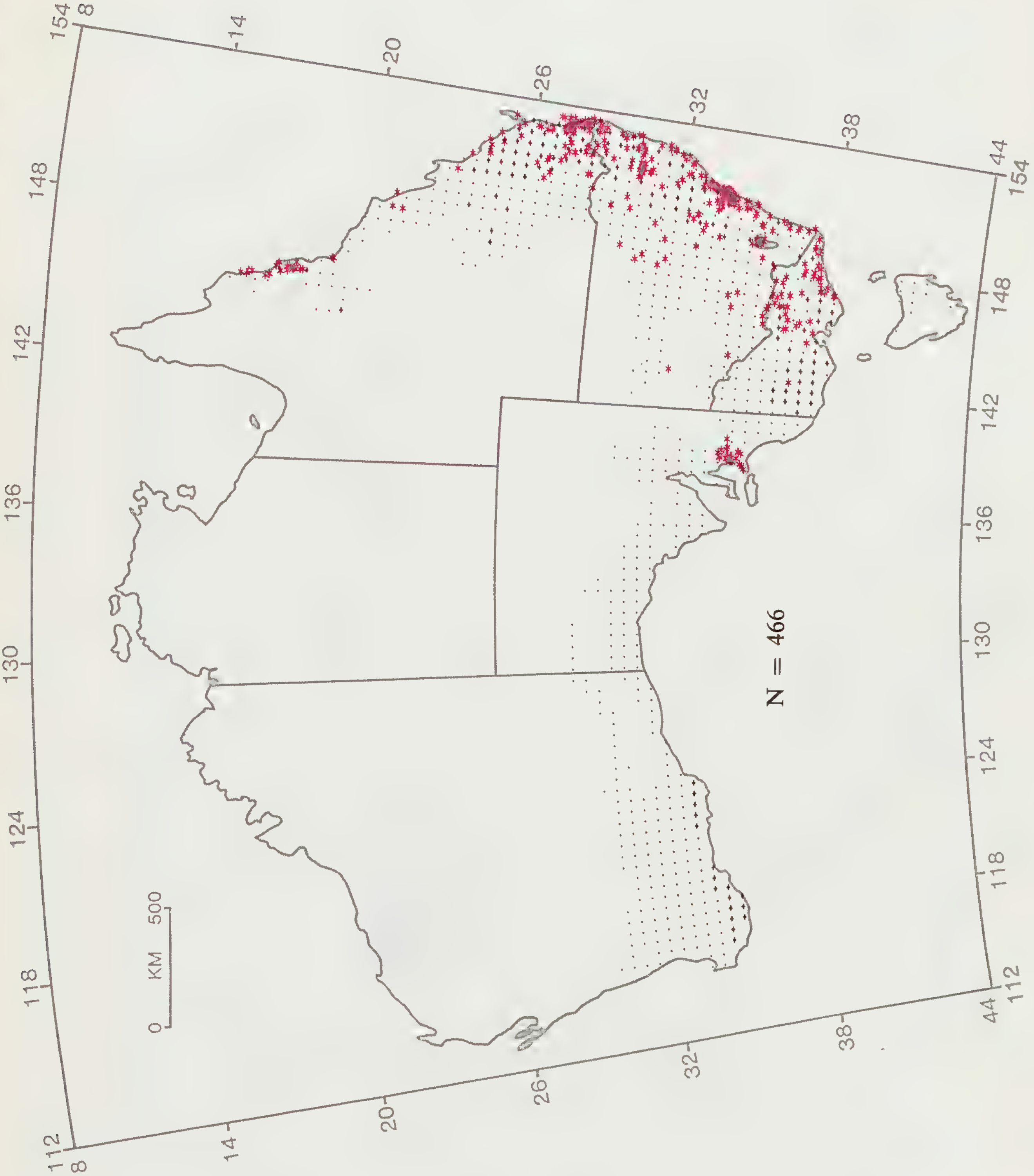



N = 49
0 KM 500
112
118
124
130
136
142
148
154
8
14
20
26
32
38
44

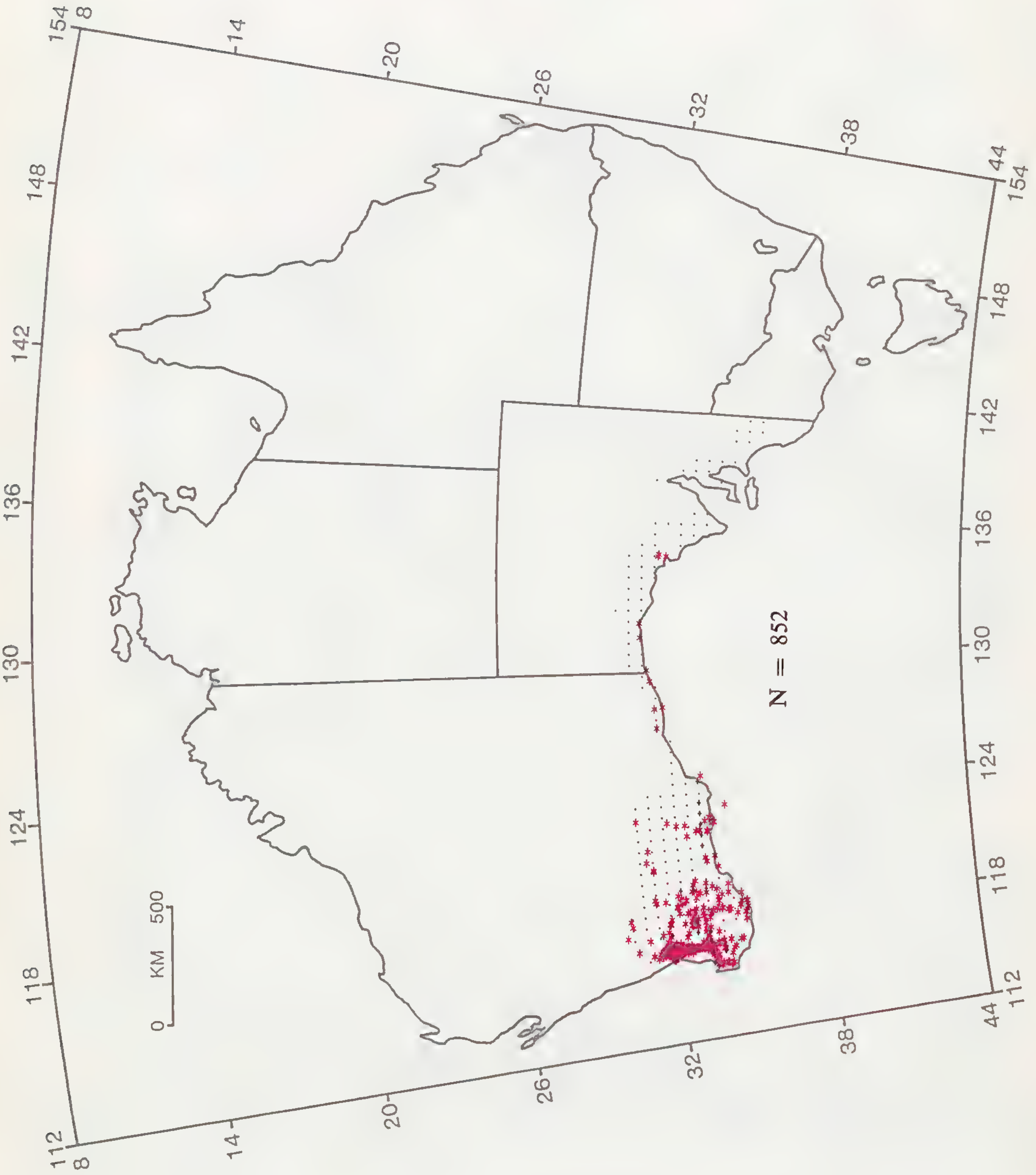
Map 48 Pseudechis guttatus

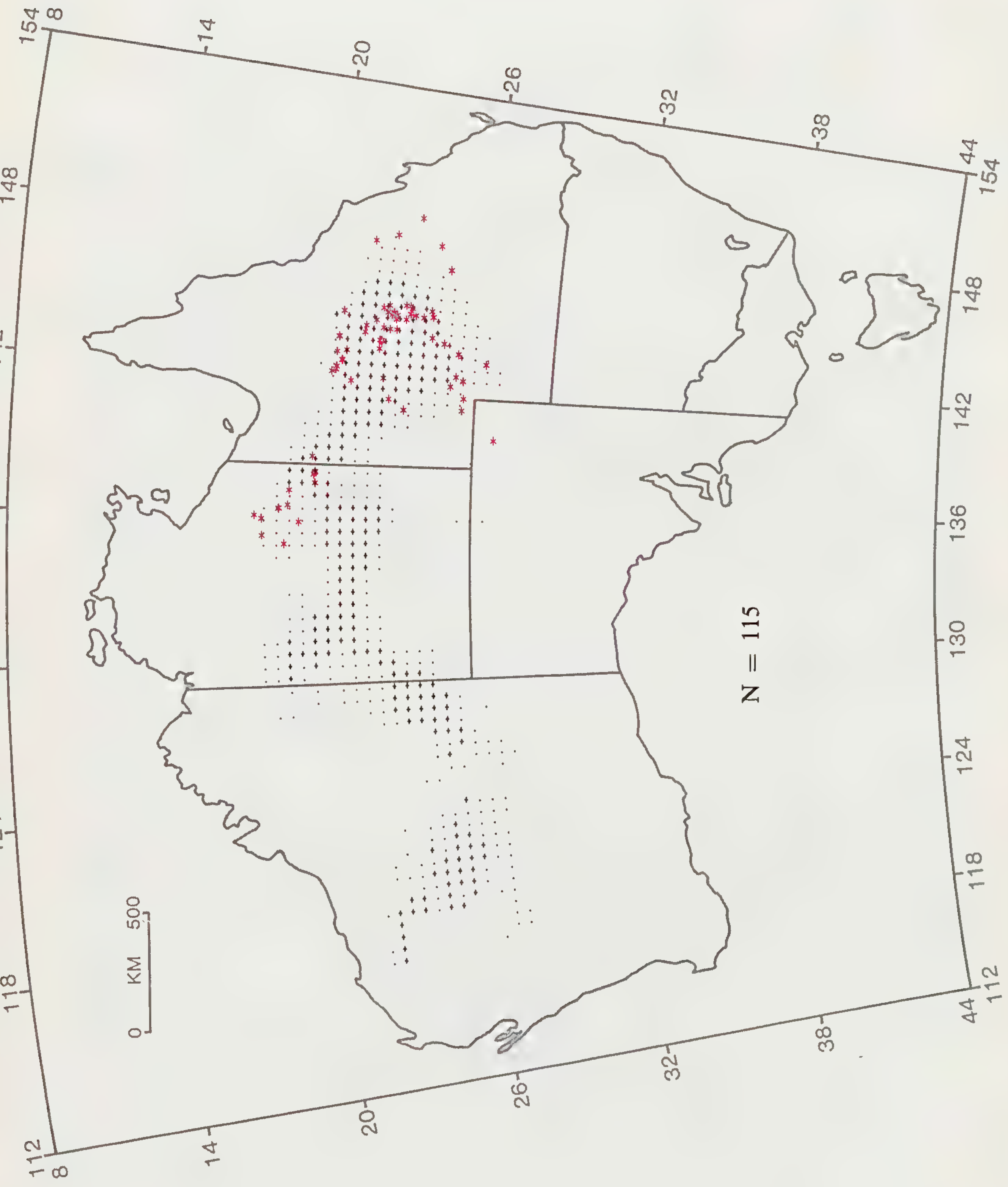


Pseudechis porphyriacus **Map 49**

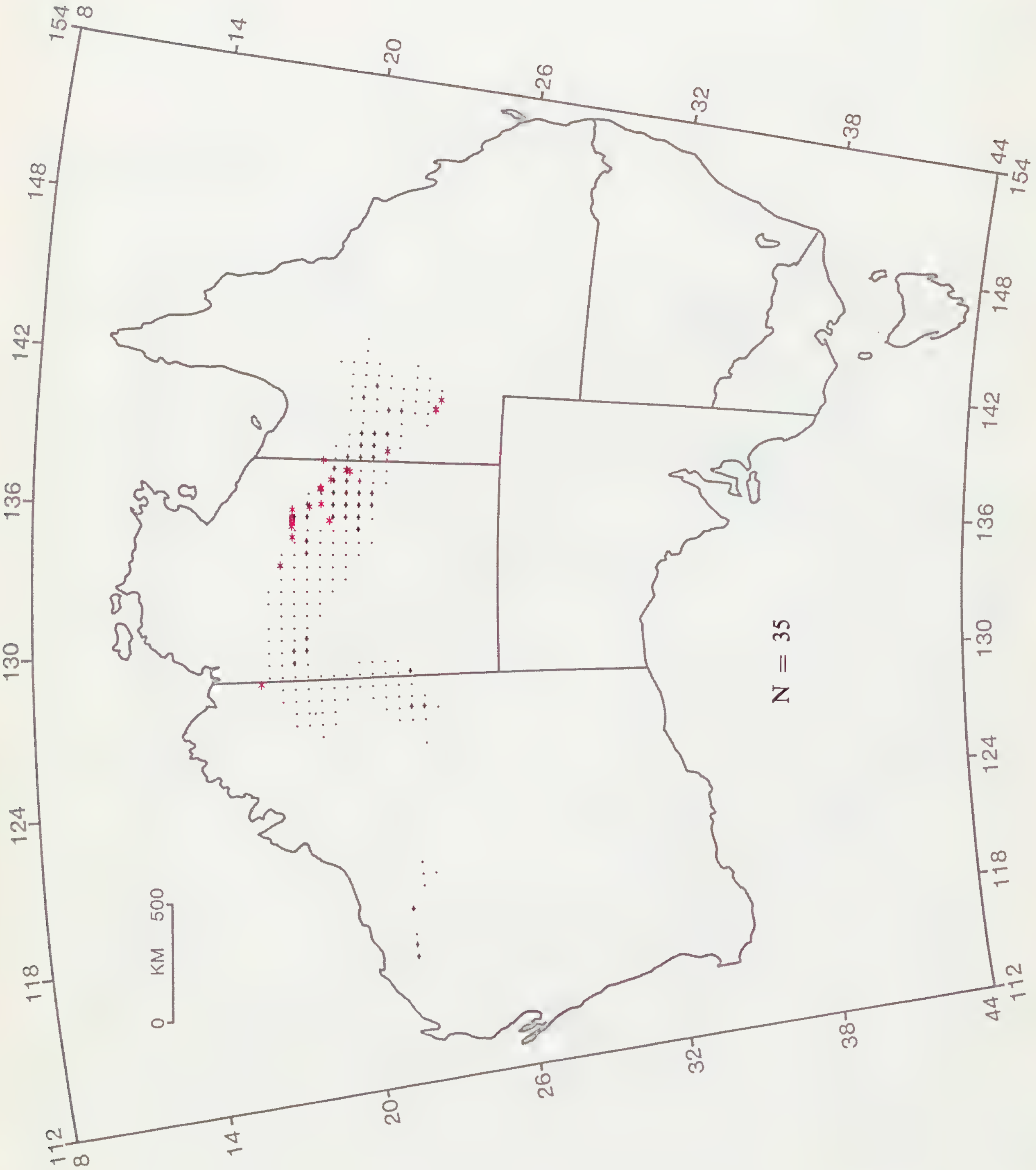


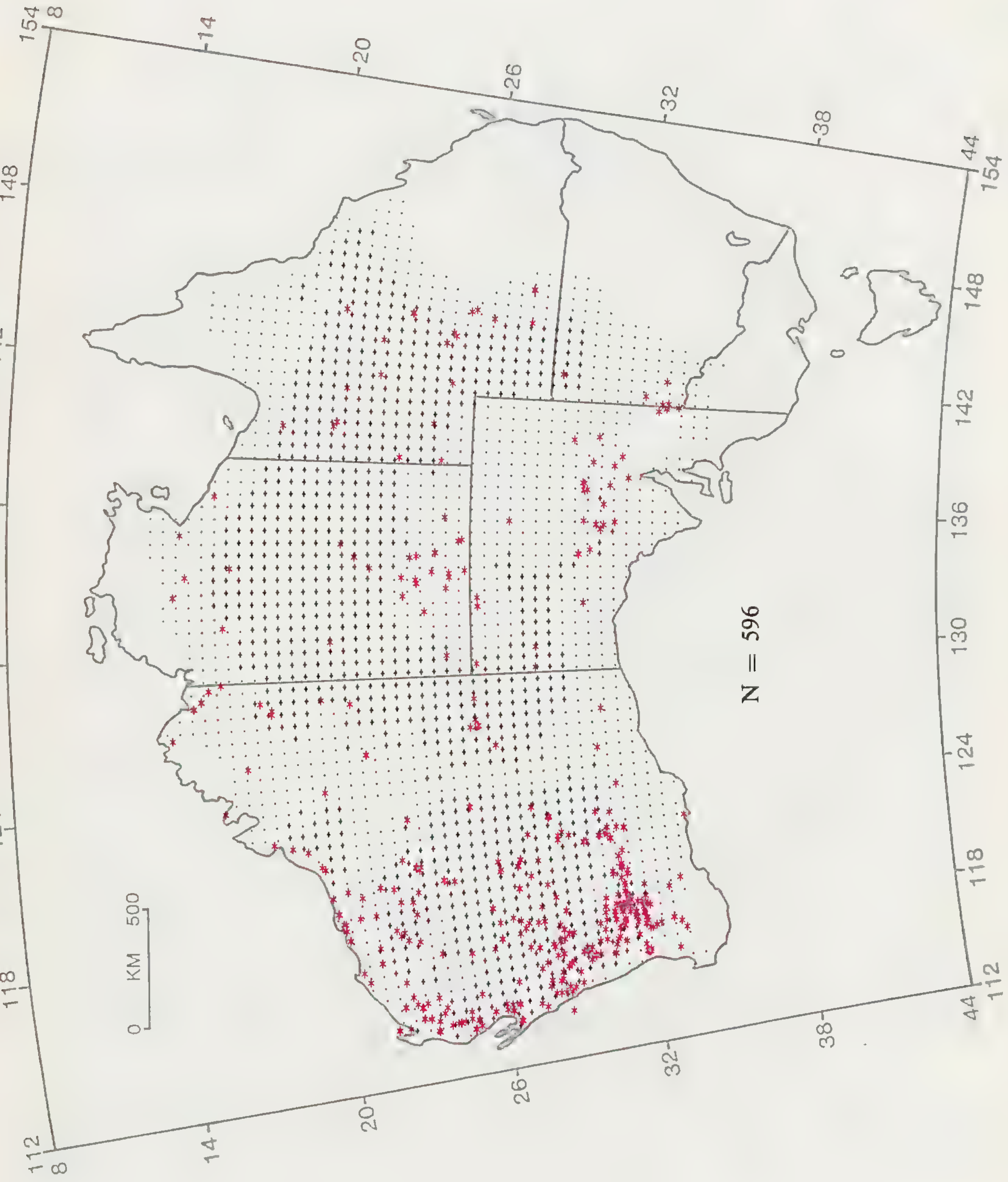
Map 50 Pseudonaja affinis



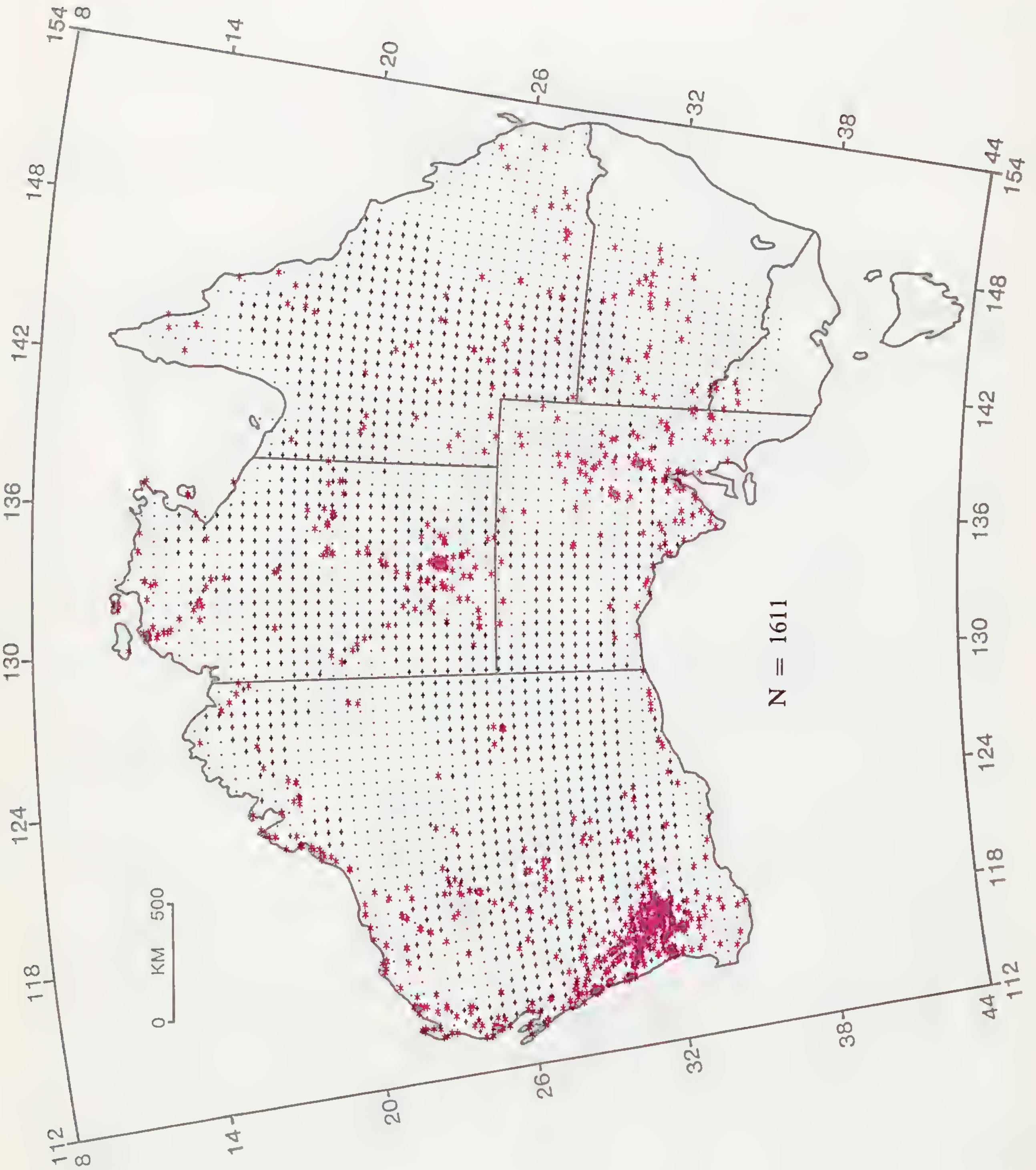

154
148
142
136
130
124
118
112
8
14
20
26
32
38
44
0 KM 500
N = 115

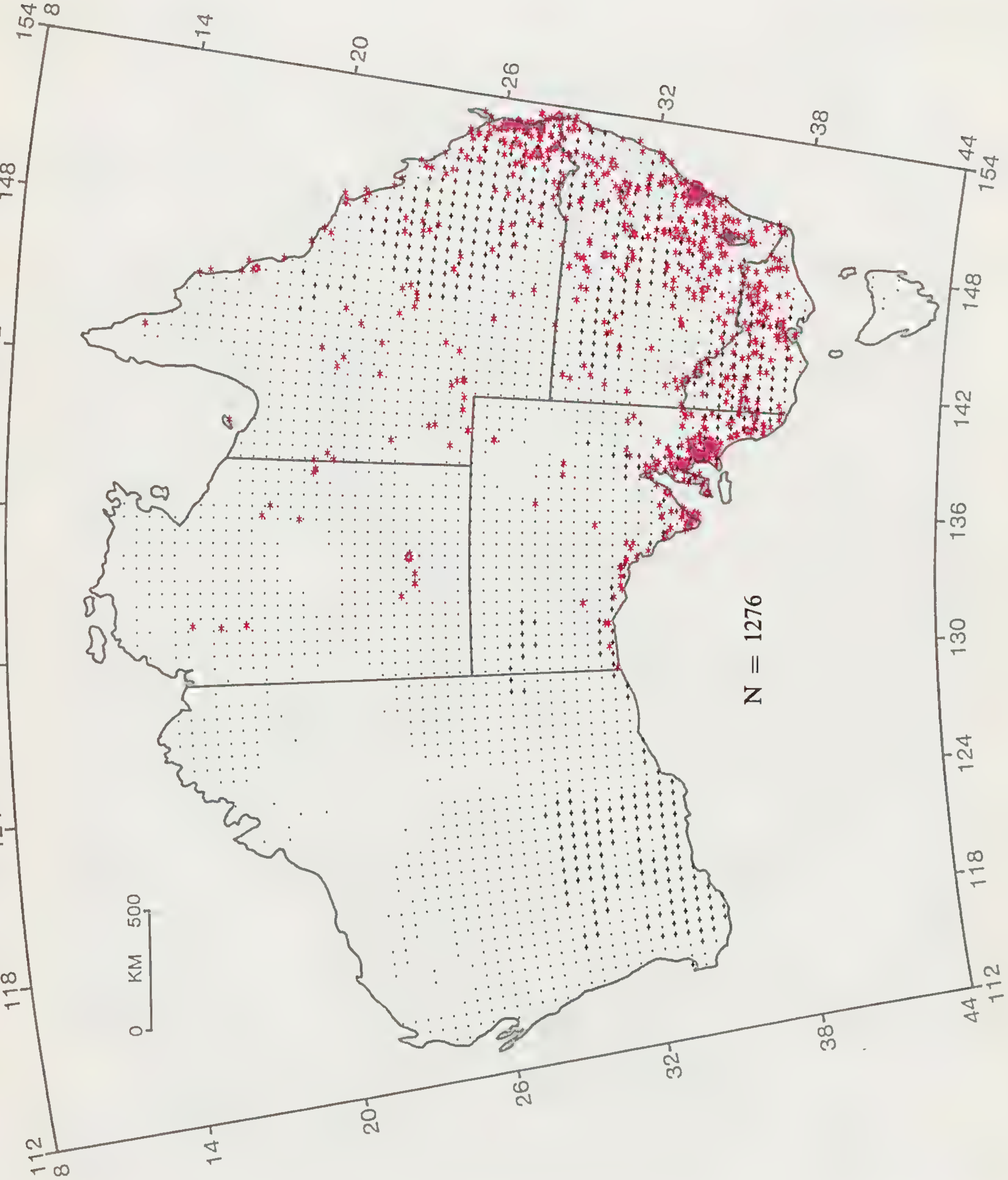
Map 52 Pseudonaja ingrami



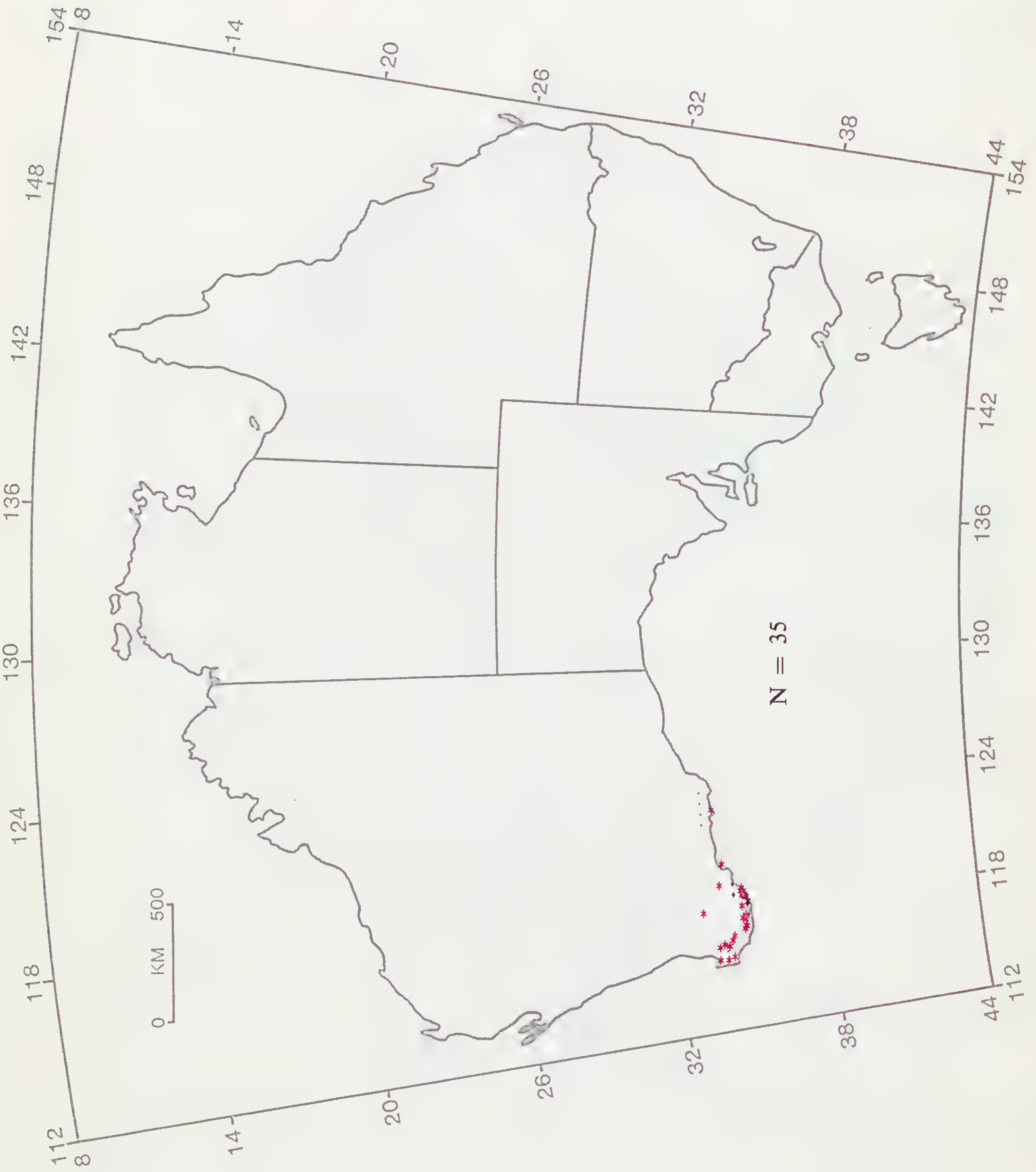

154
148
142
136
130
124
118
112
8
14
20
26
32
38
44
N = 596
0 KM 500

Map 54 Pseudonaja nuchalis

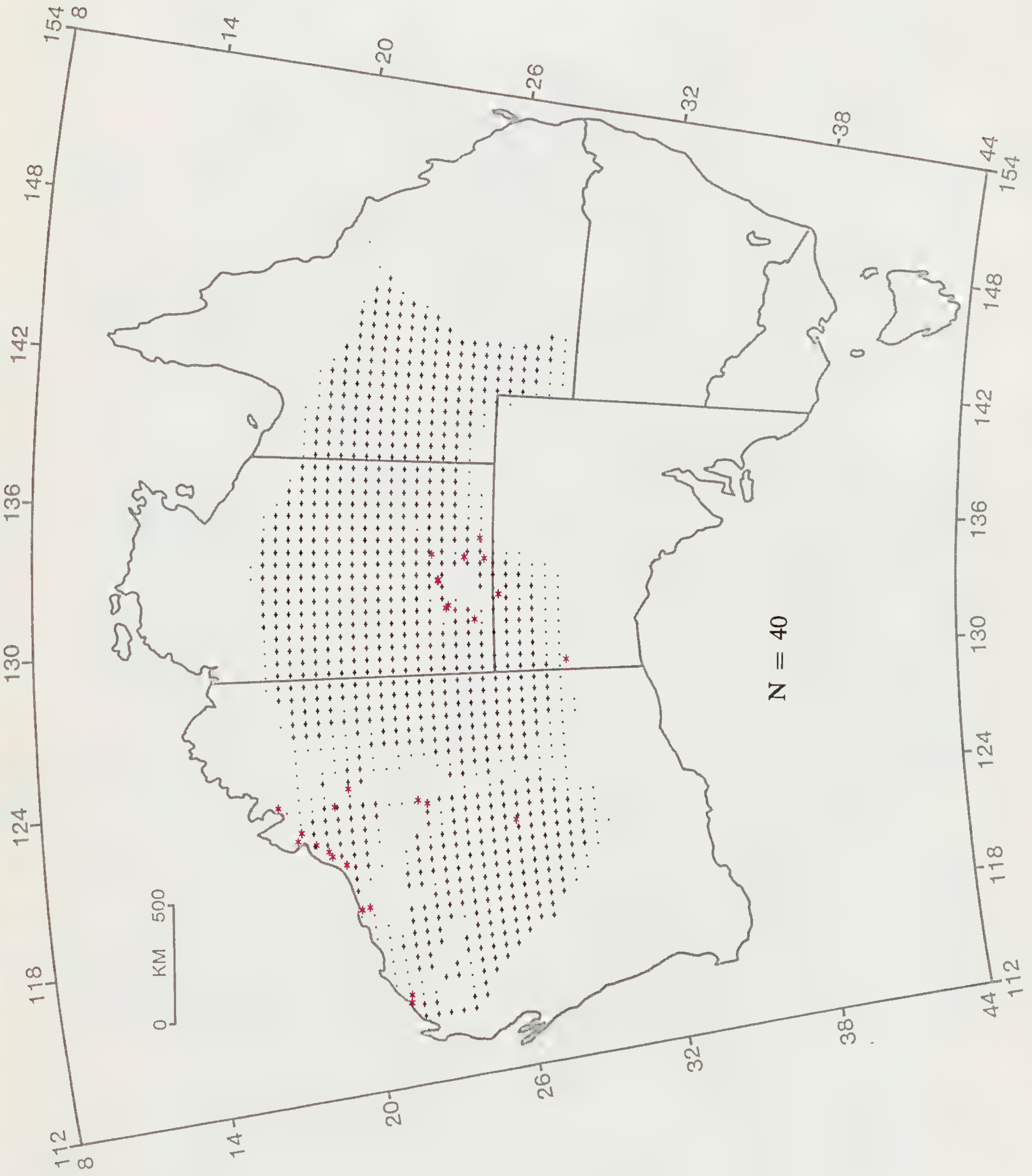



154
8
14
20
26
32
38
44
154
148
142
136
130
124
118
112
44
38
32
26
20
14
8
112
118
124
130
136
142
148
0 KM 500
N = 1276

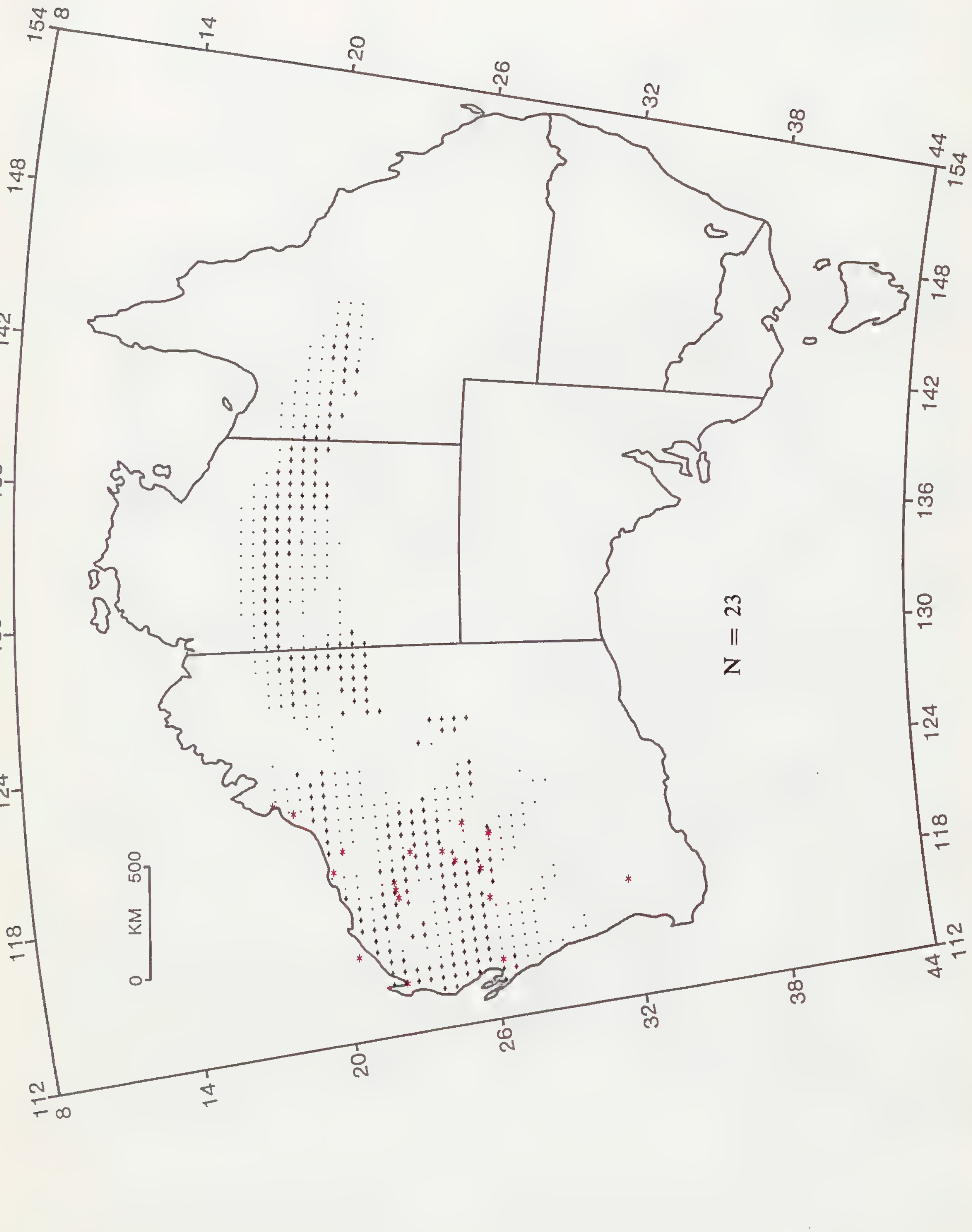
Map 56 Rhinoplocephalus bicolor

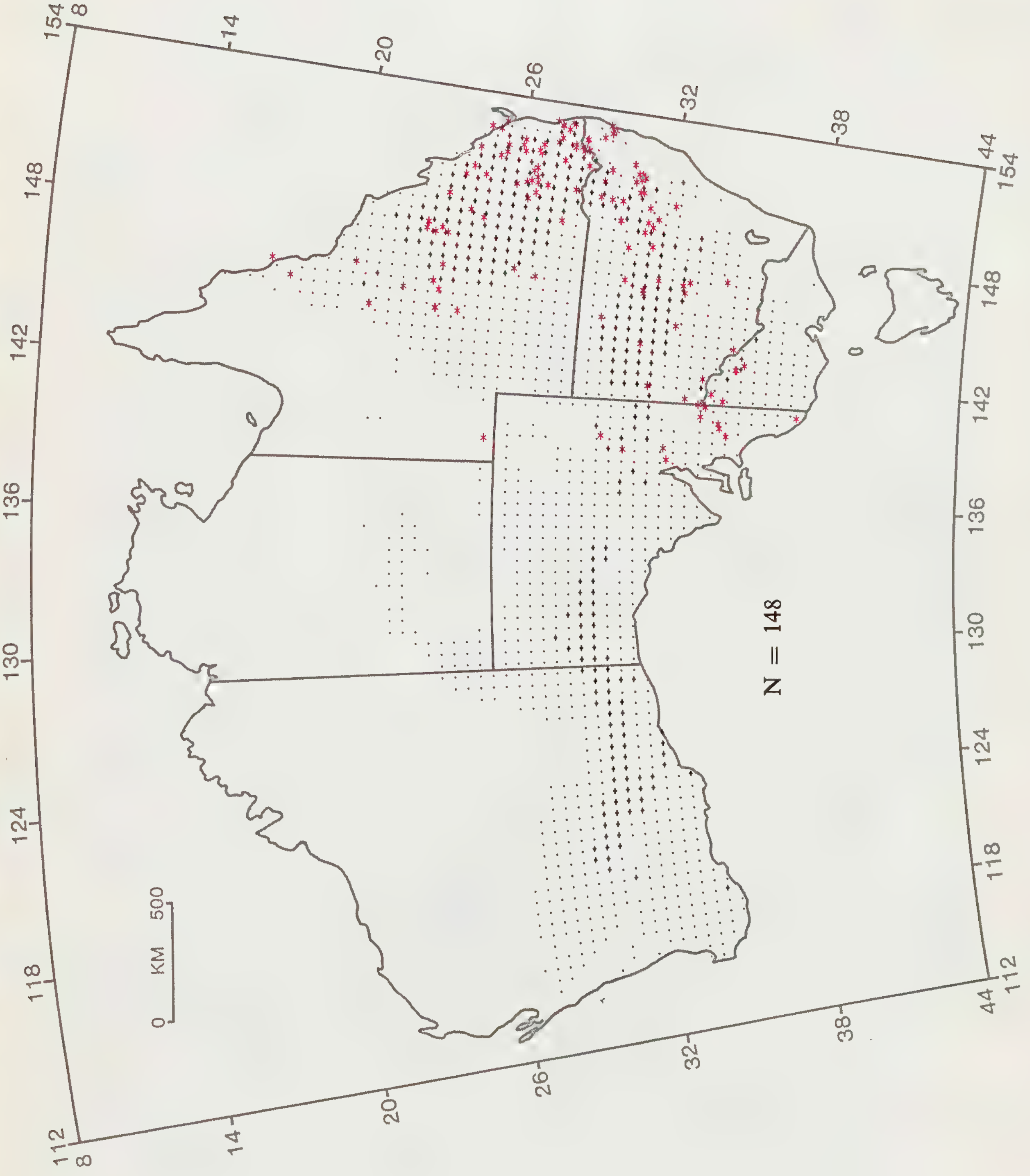


Simoselaps anomalus **Map 57**

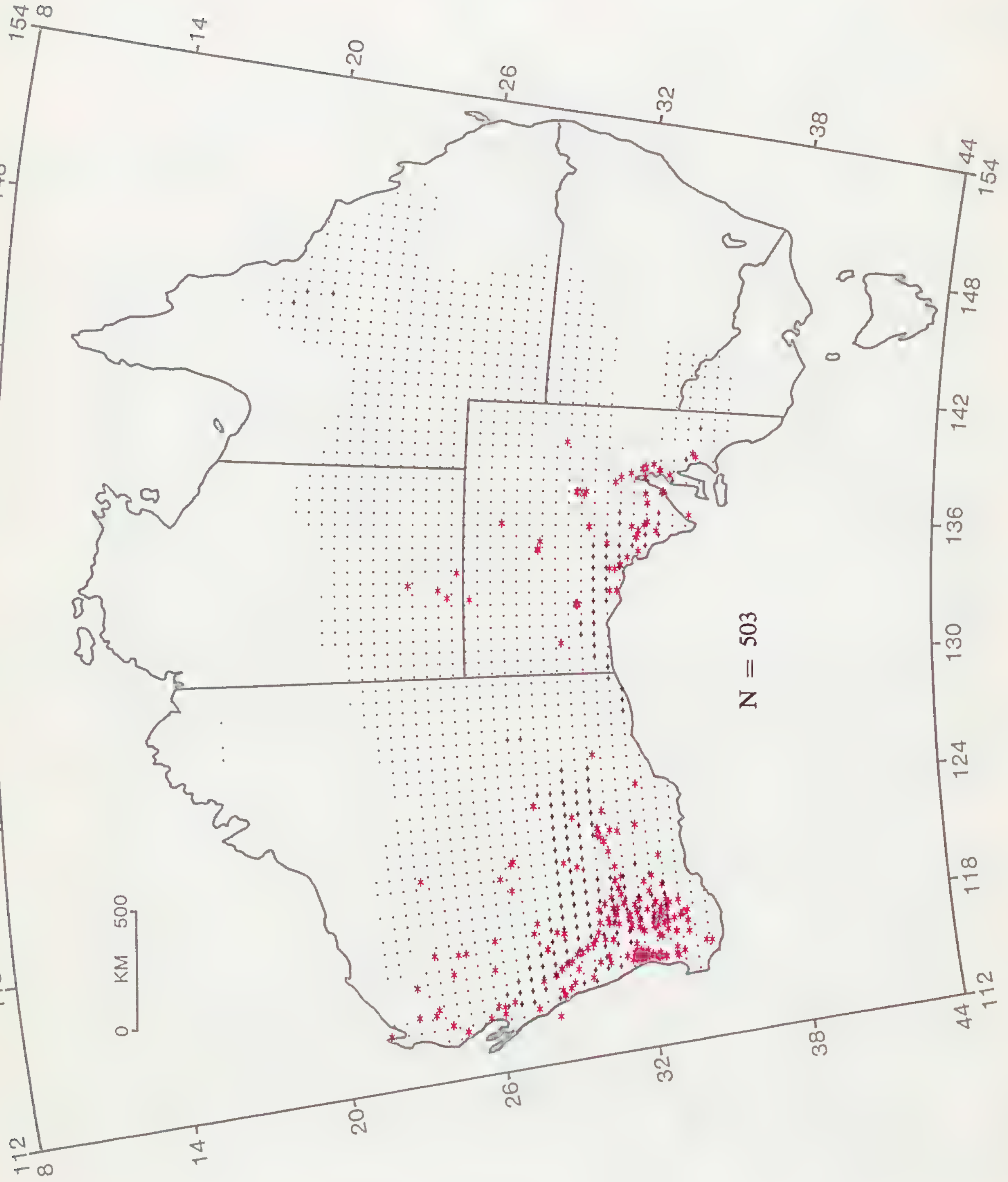


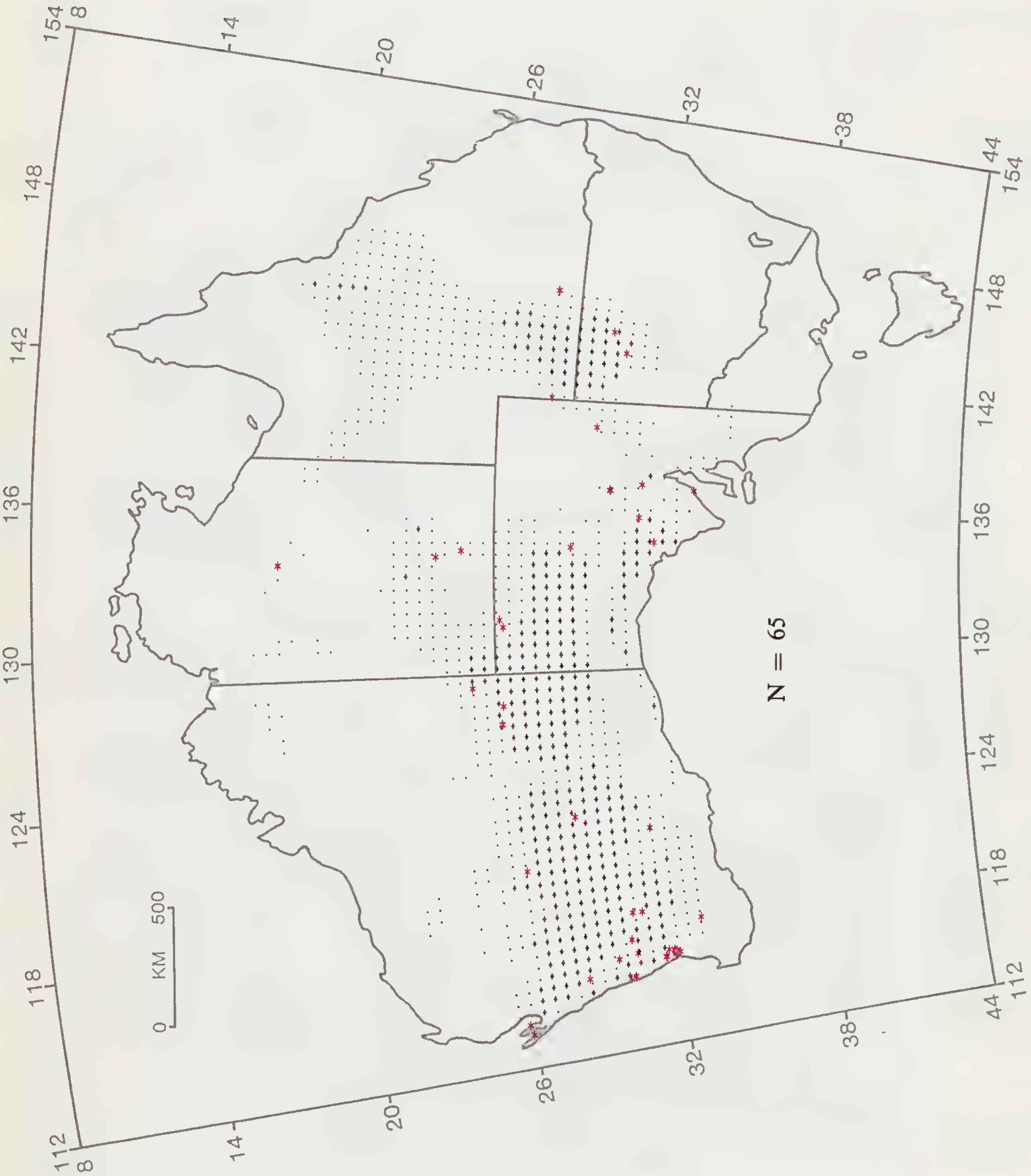
Map 58 Simoseelaps approximans



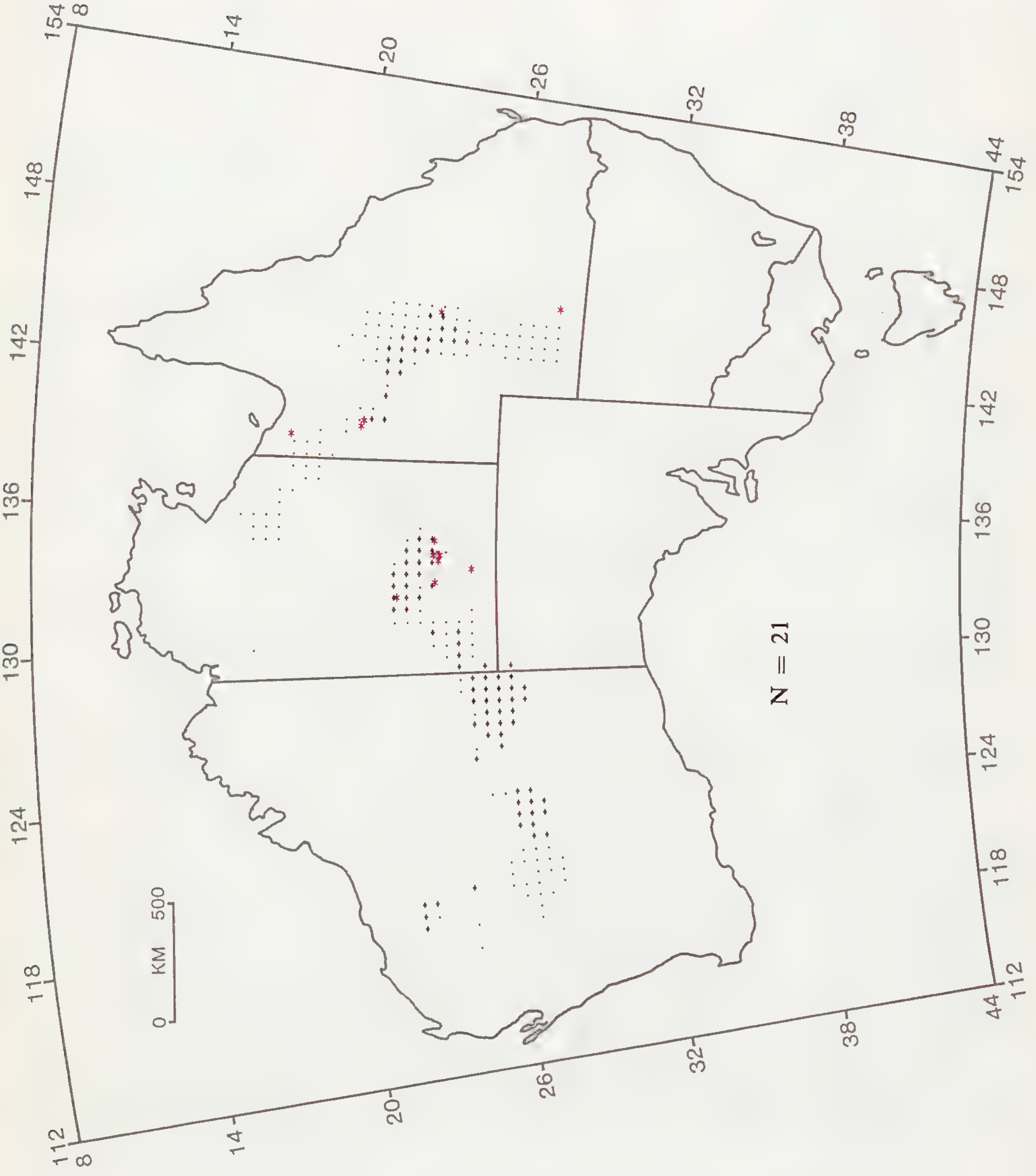

N = 148
0 KM 500
8
14
20
26
32
38
44
112
118
124
130
136
142
148
154

Map 60 Simoselaps bertholdi

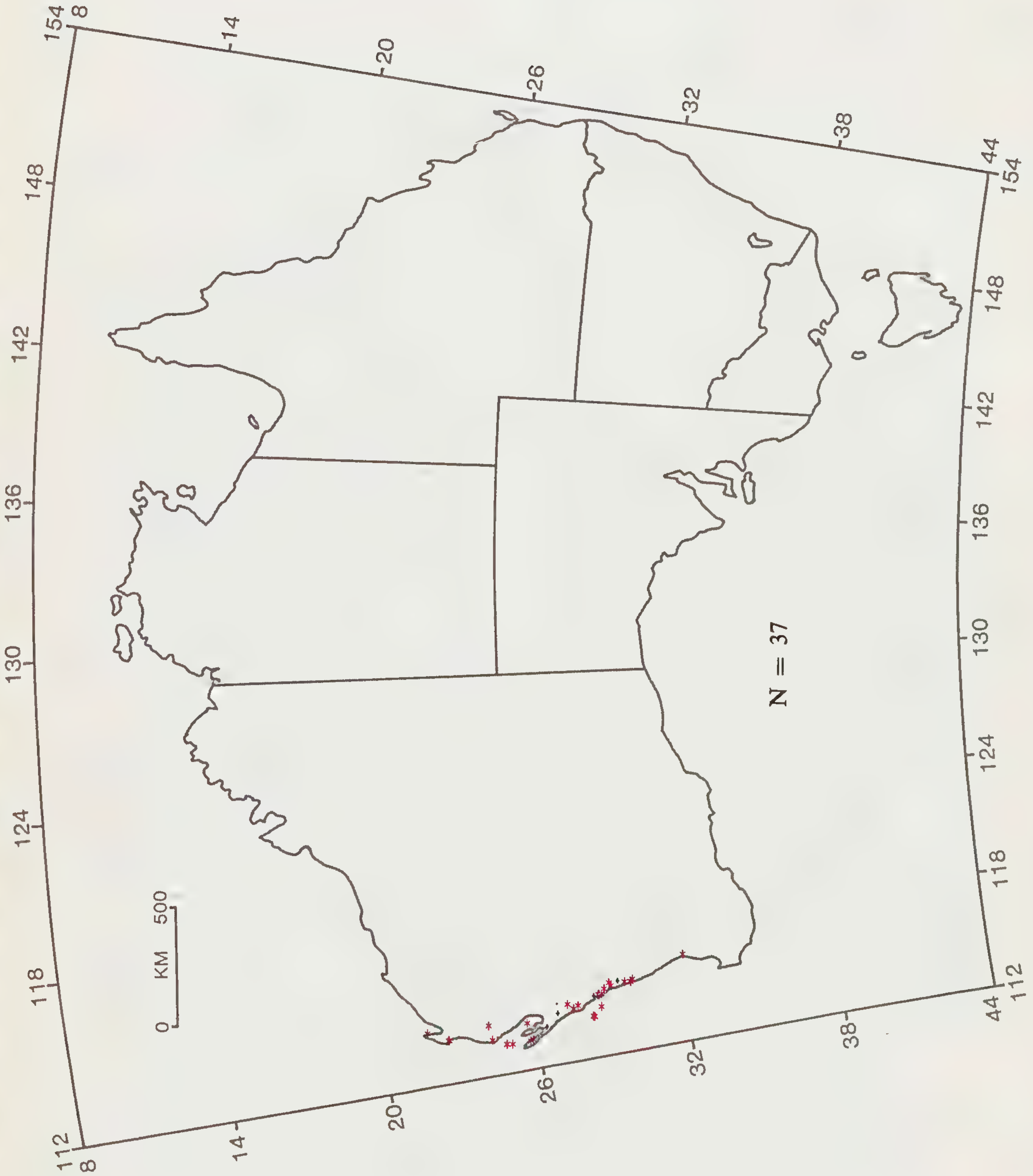



154
8
14
20
26
32
38
44
154
148
142
136
130
124
118
112
44
38
32
26
20
14
8
112
118
124
130
136
142
148
N = 65
0 KM 500

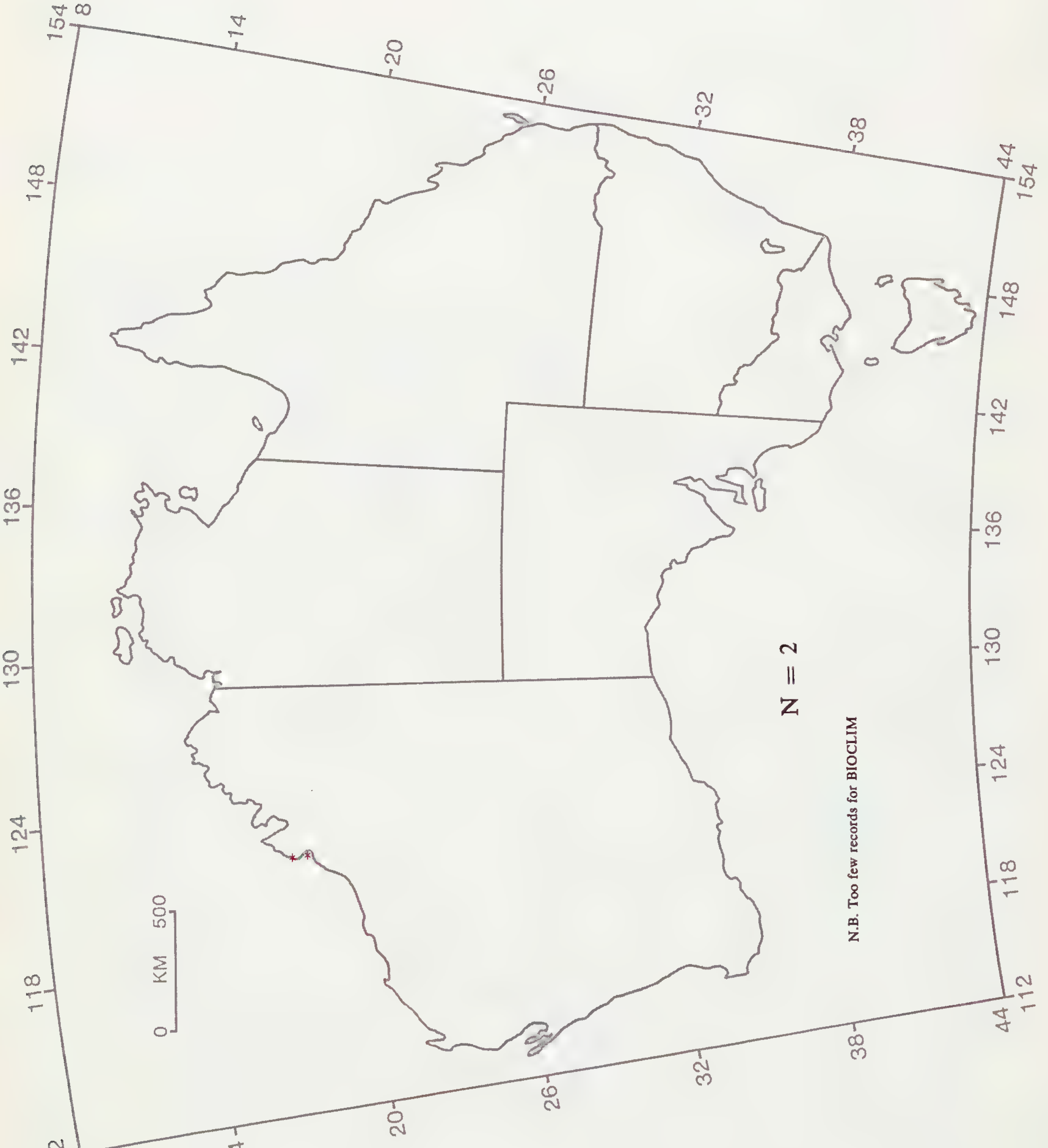
Map 62 Simoselaps incinctus



Simoselaps littoralis **Map 63**

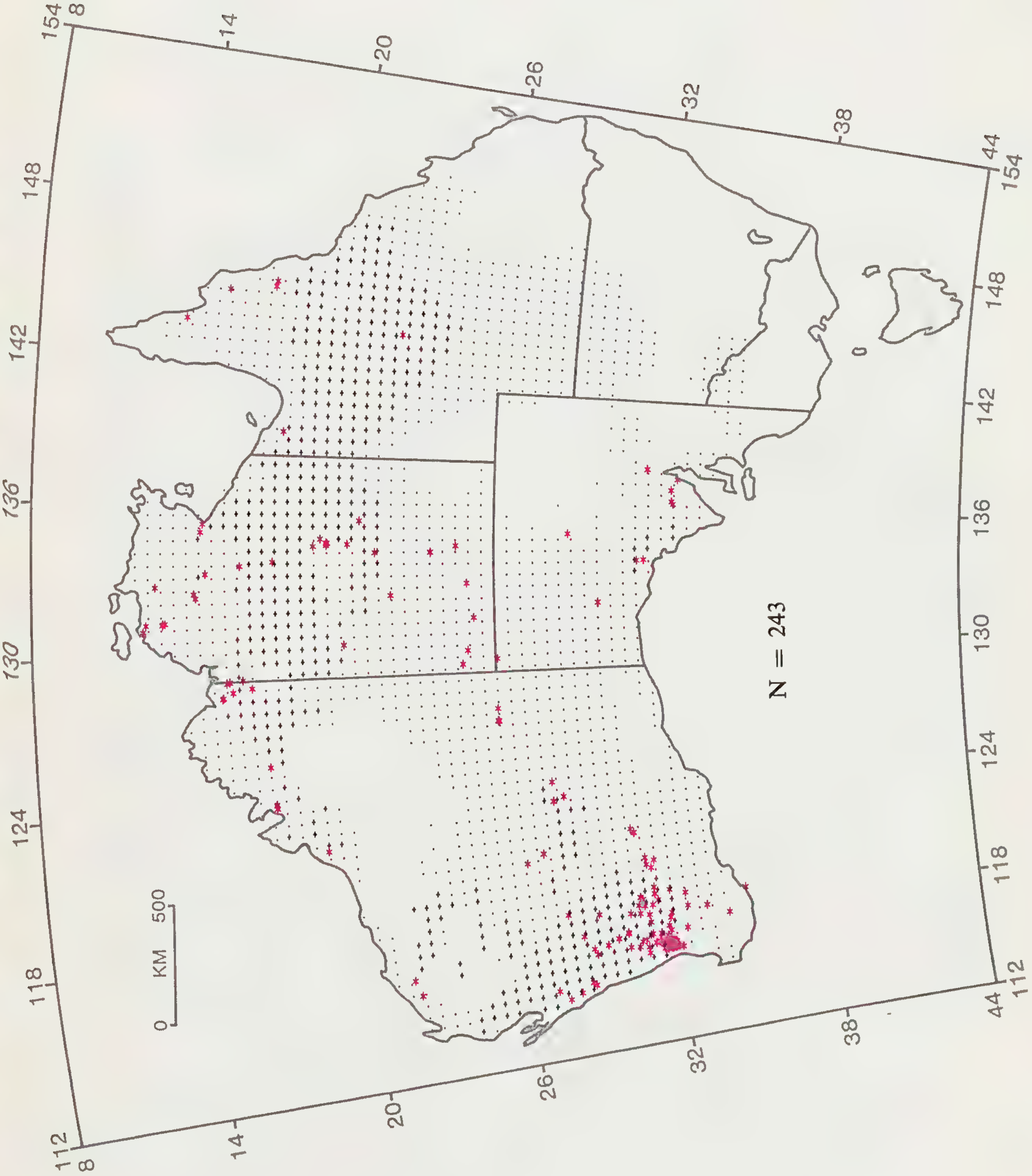


Map 64 Simoselaps minimus



N = 2

N.B. Too few records for BIOCLIM


N = 243
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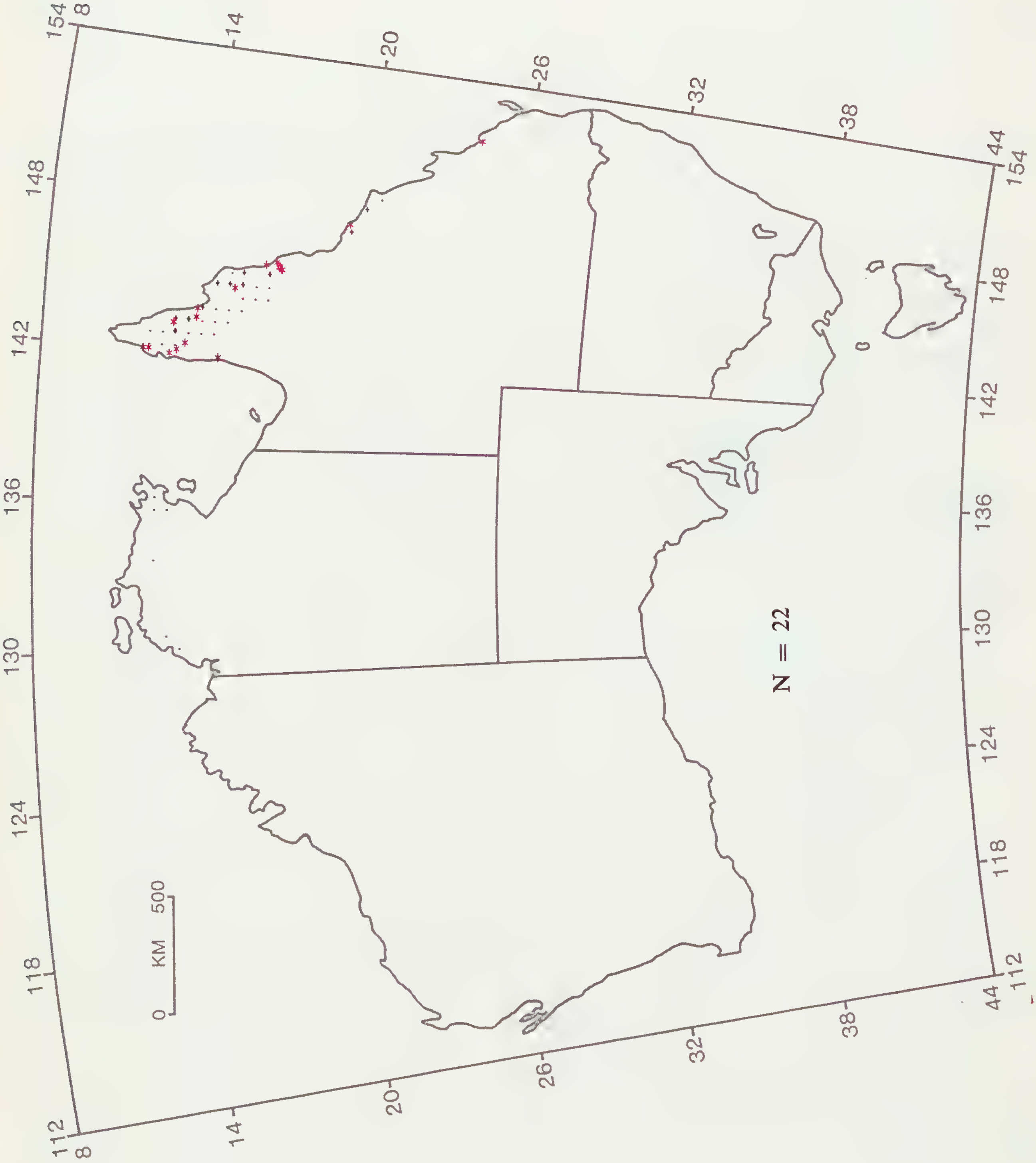
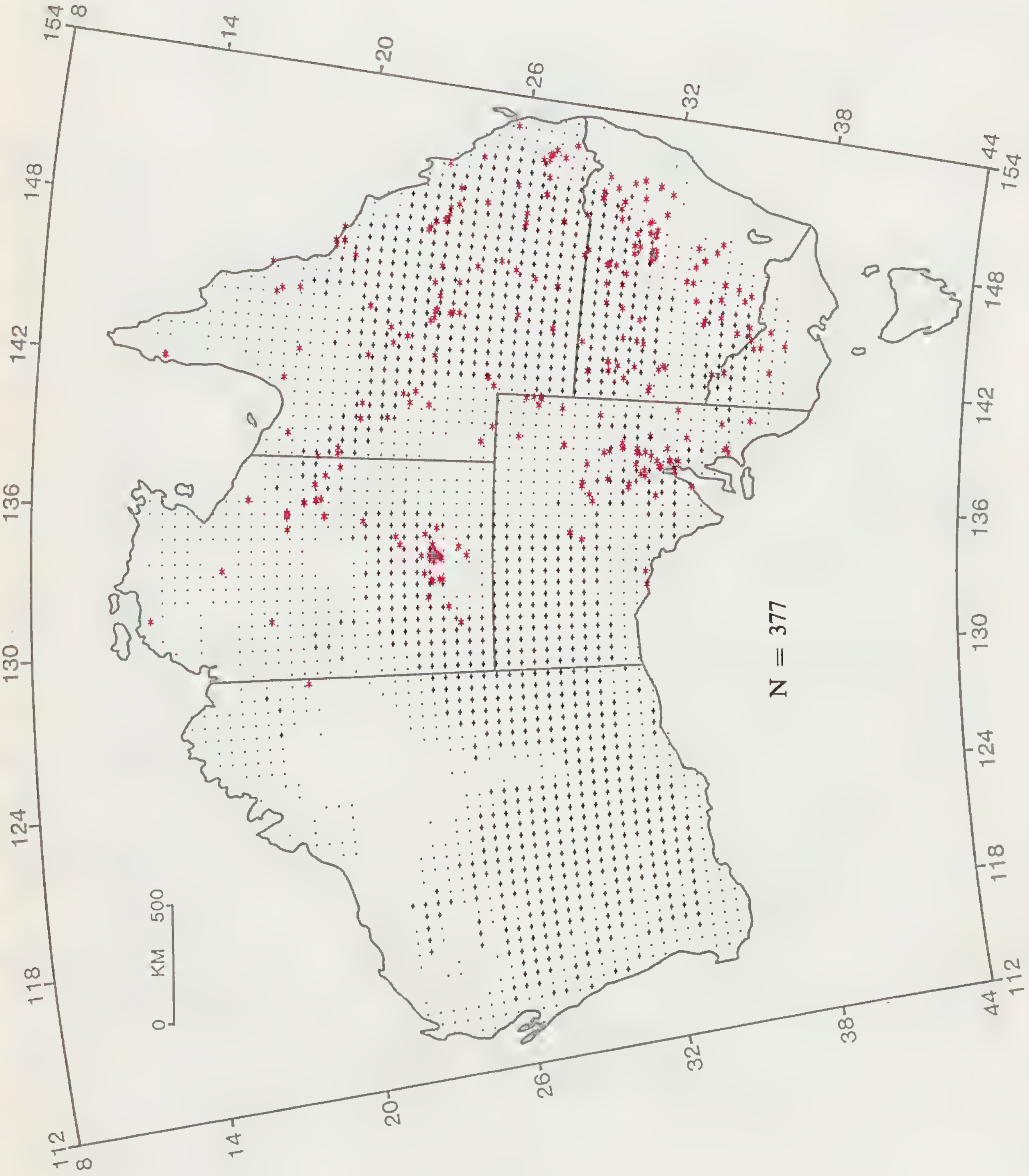
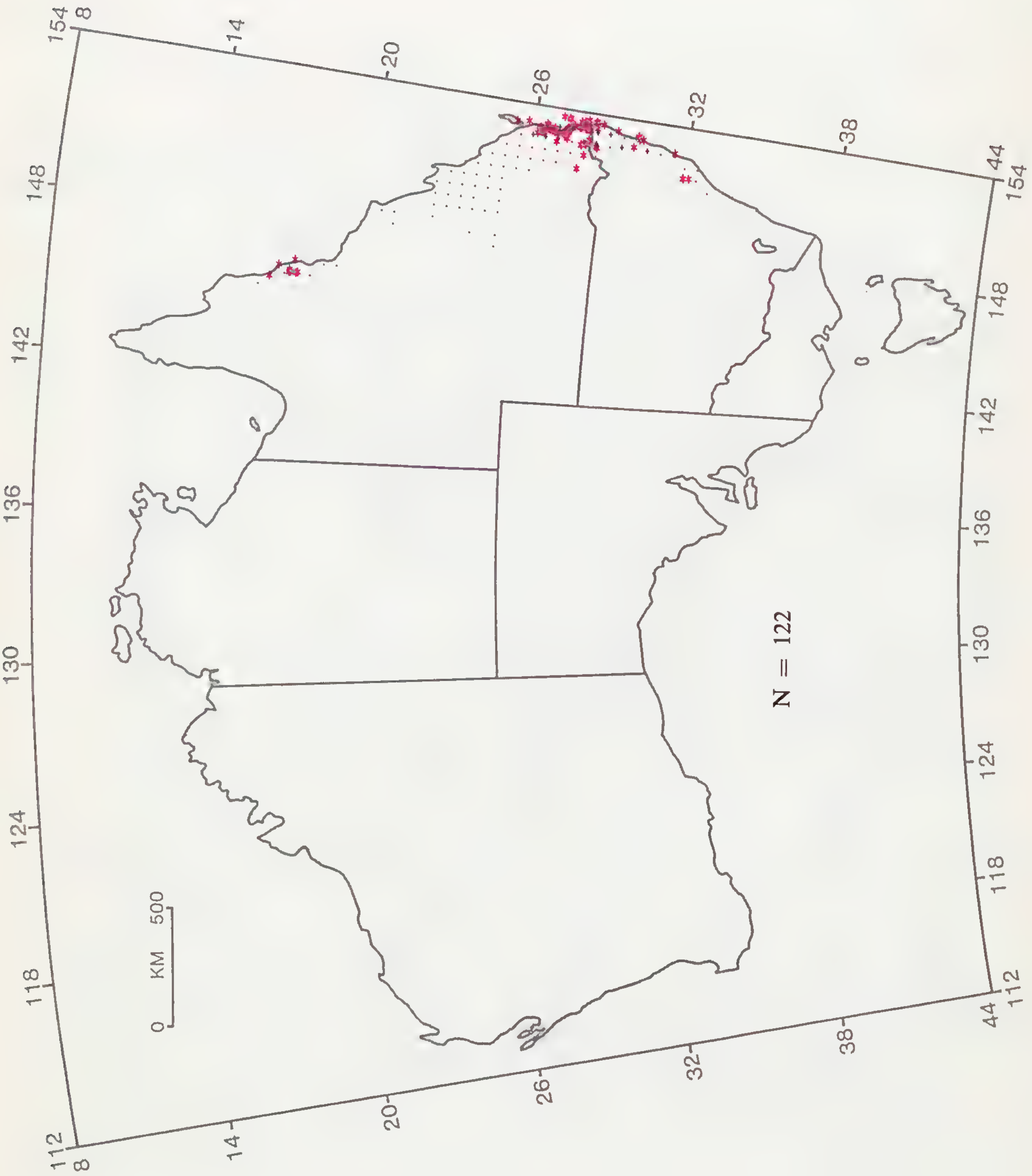
14
20
26
32
38
44
112
118
124
130
136
142
148
154

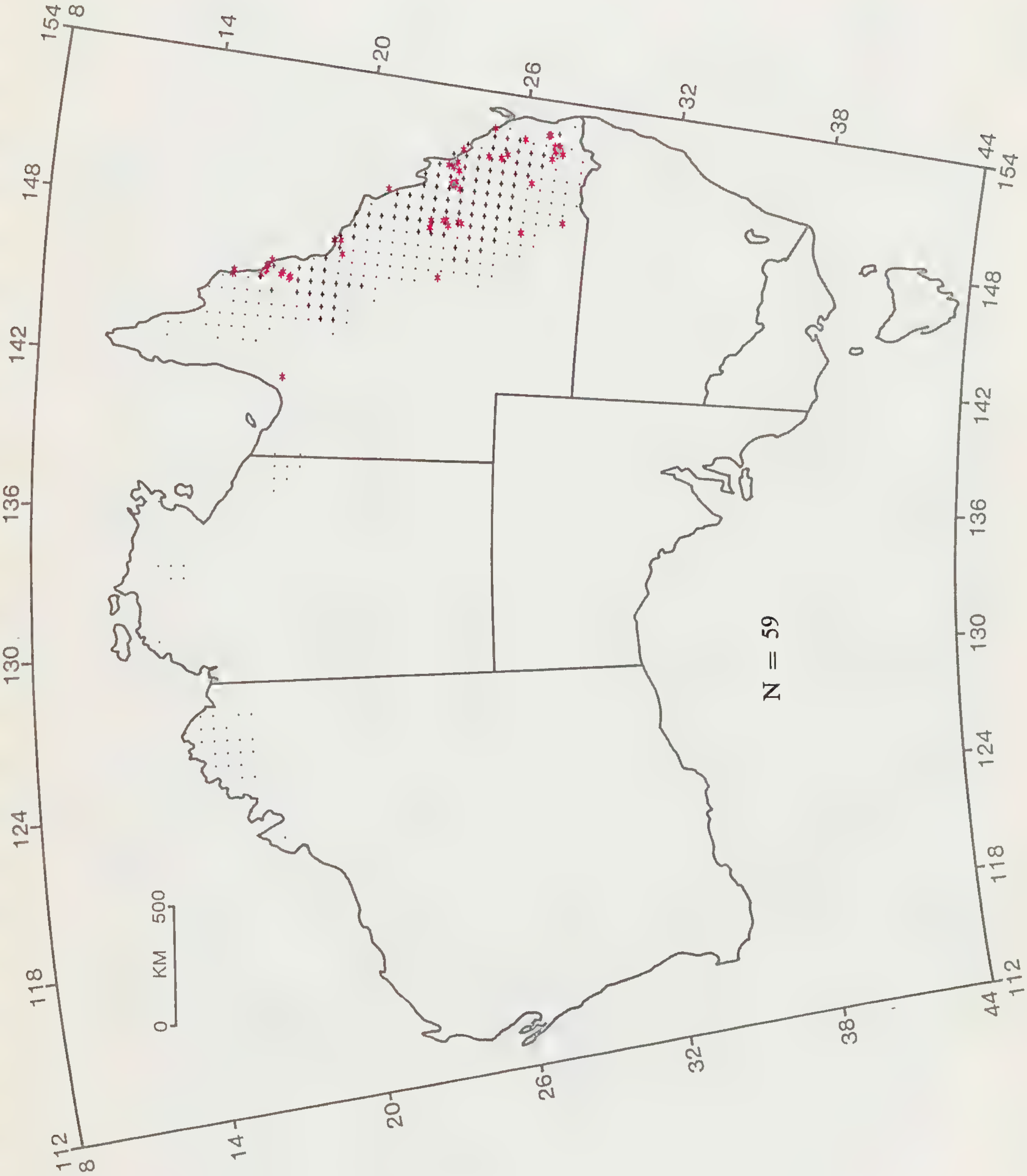
Map 66 Simoselaps warro




154
8
14
20
26
32
38
44
154
148
142
136
130
124
118
112
44
38
32
26
20
14
8
112
118
124
130
136
142
148
0 KM 500
N = 377

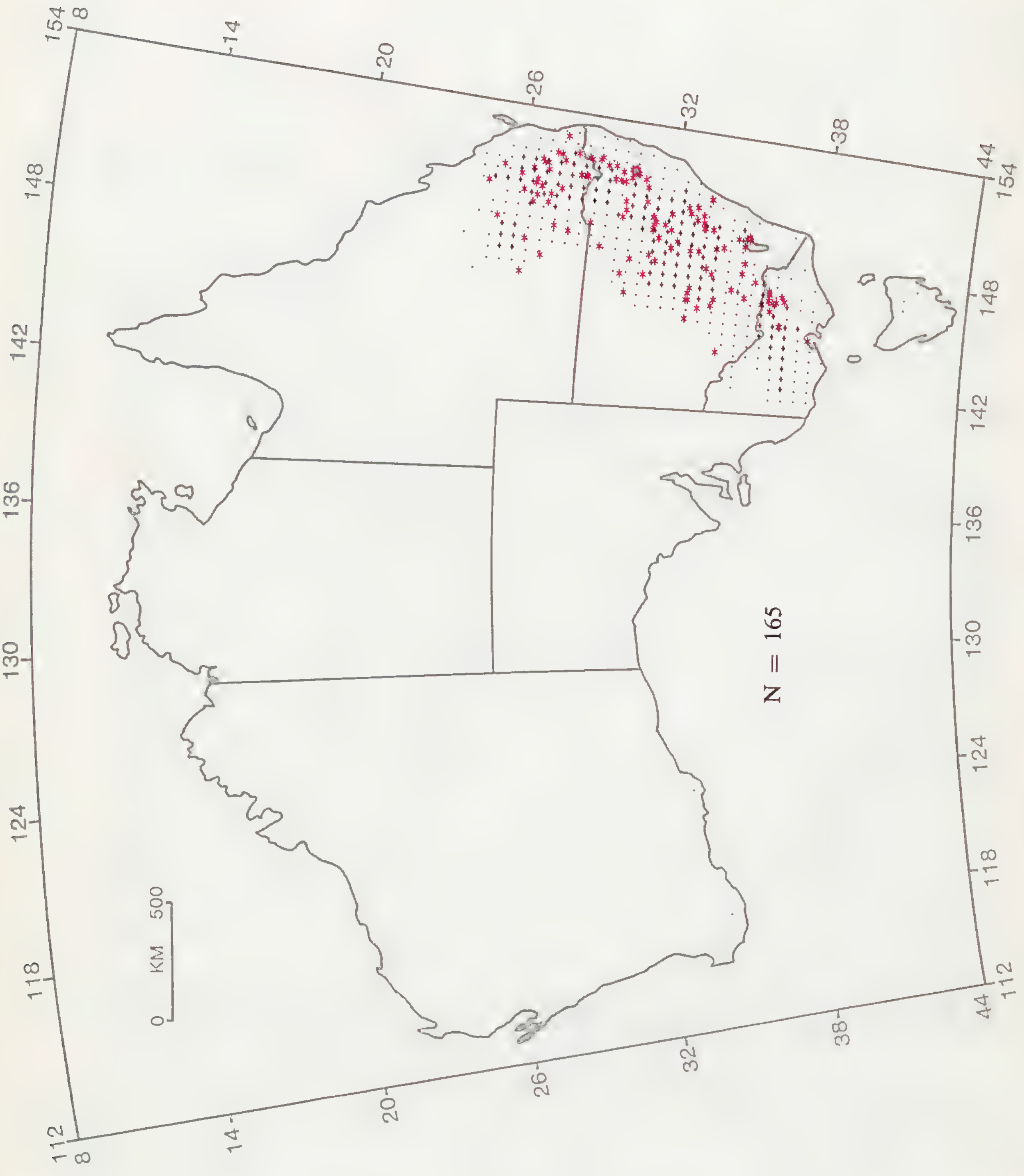
Map 68 Tropidechis carinatus

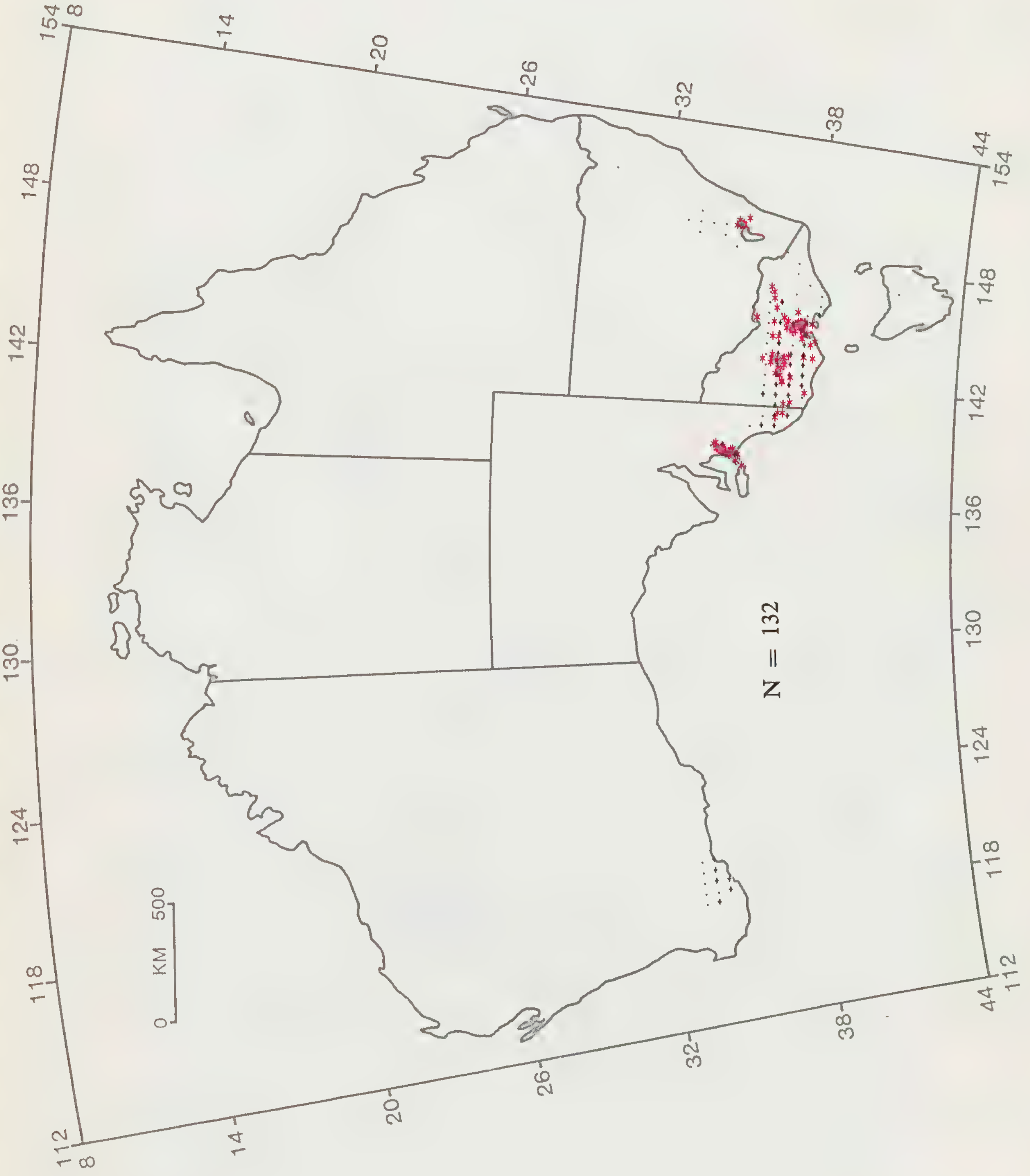




N = 59
0
KM
500
8
14
20
26
32
38
44
112
118
124
130
136
142
148
154

Map 70 Unechis dwyeri




N = 132
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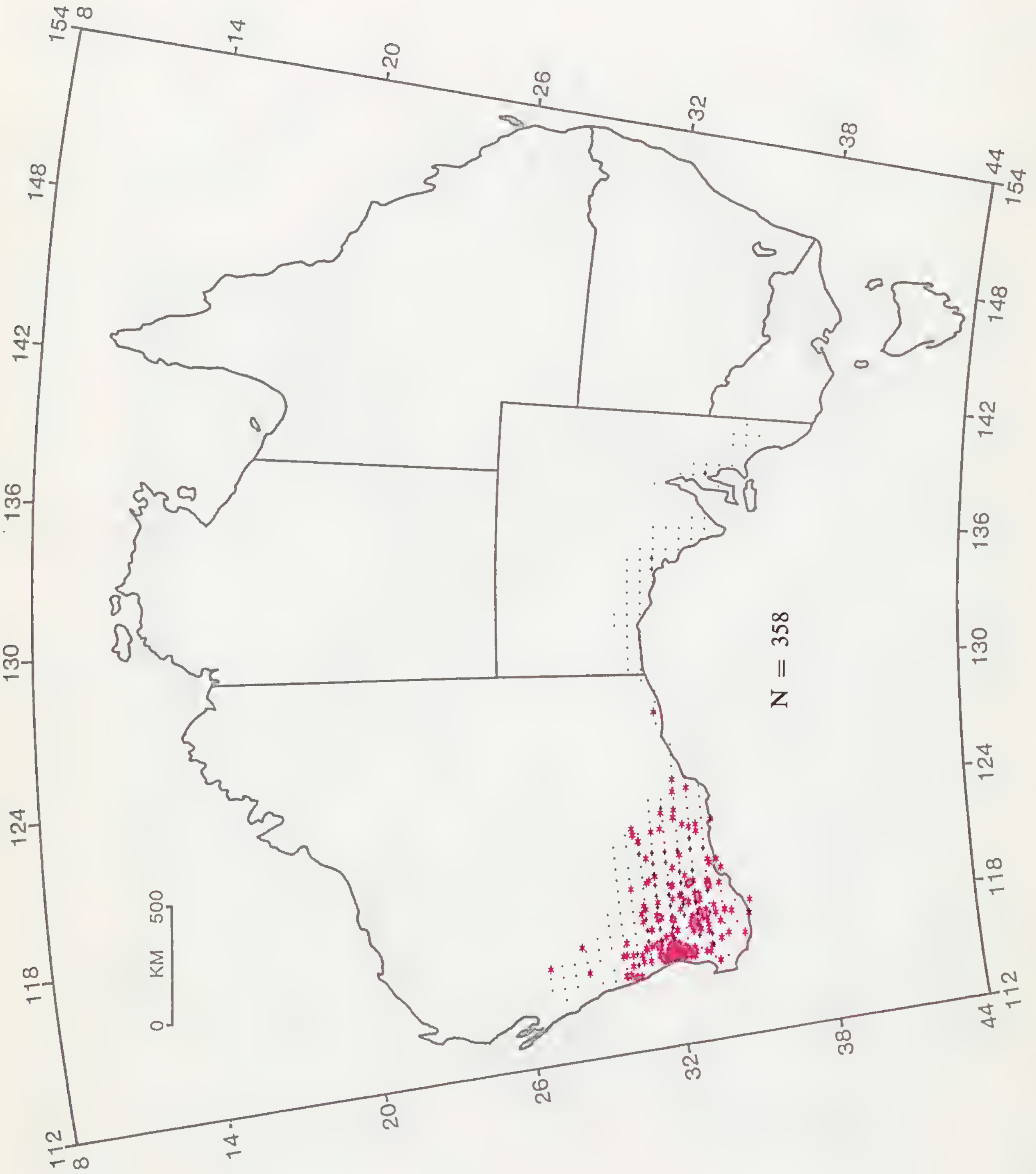
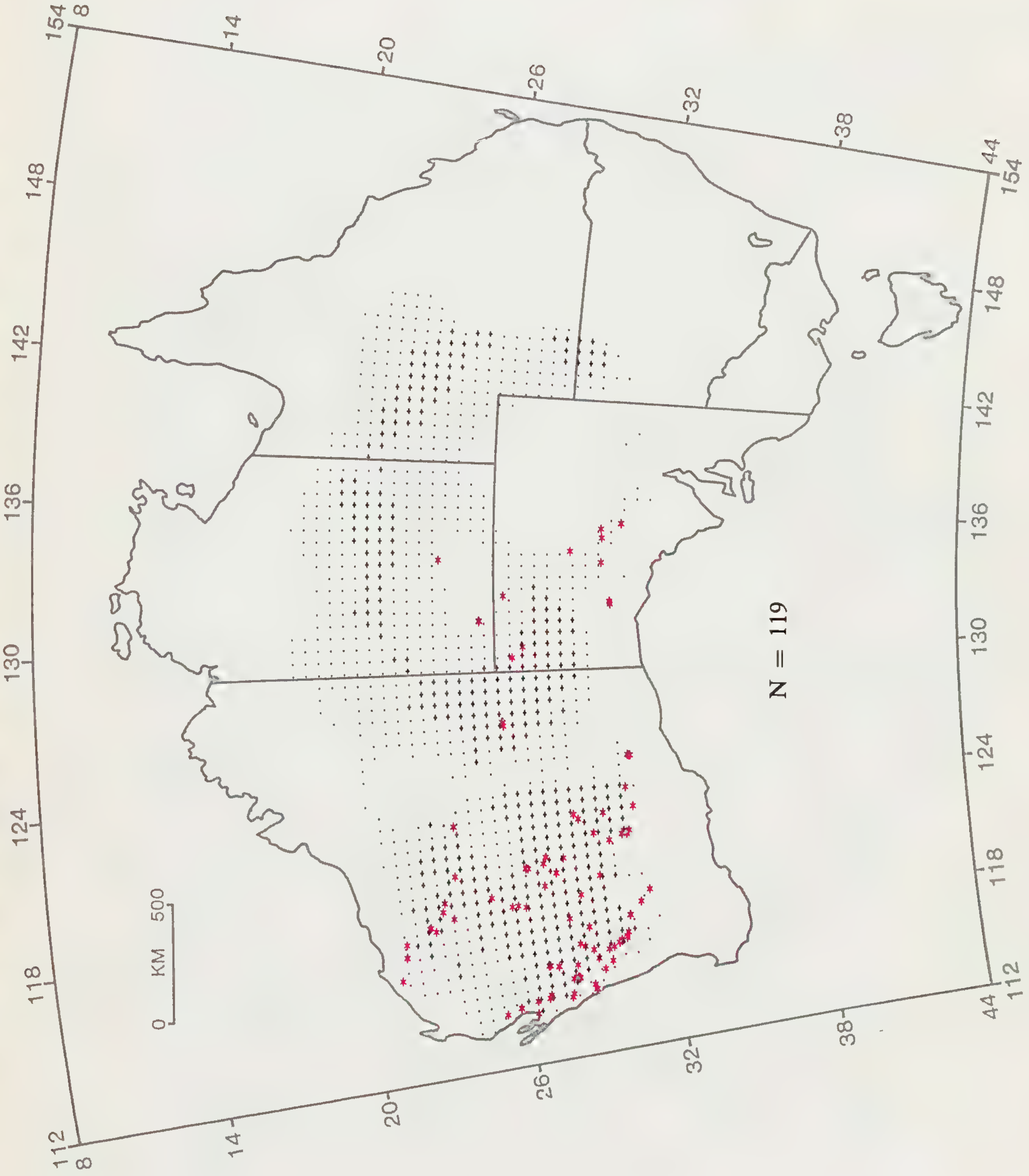
112
118
124
130
136
142
148
154
8
14
20
26
32
38
44

Map 72 Unechis gouldii




N = 119
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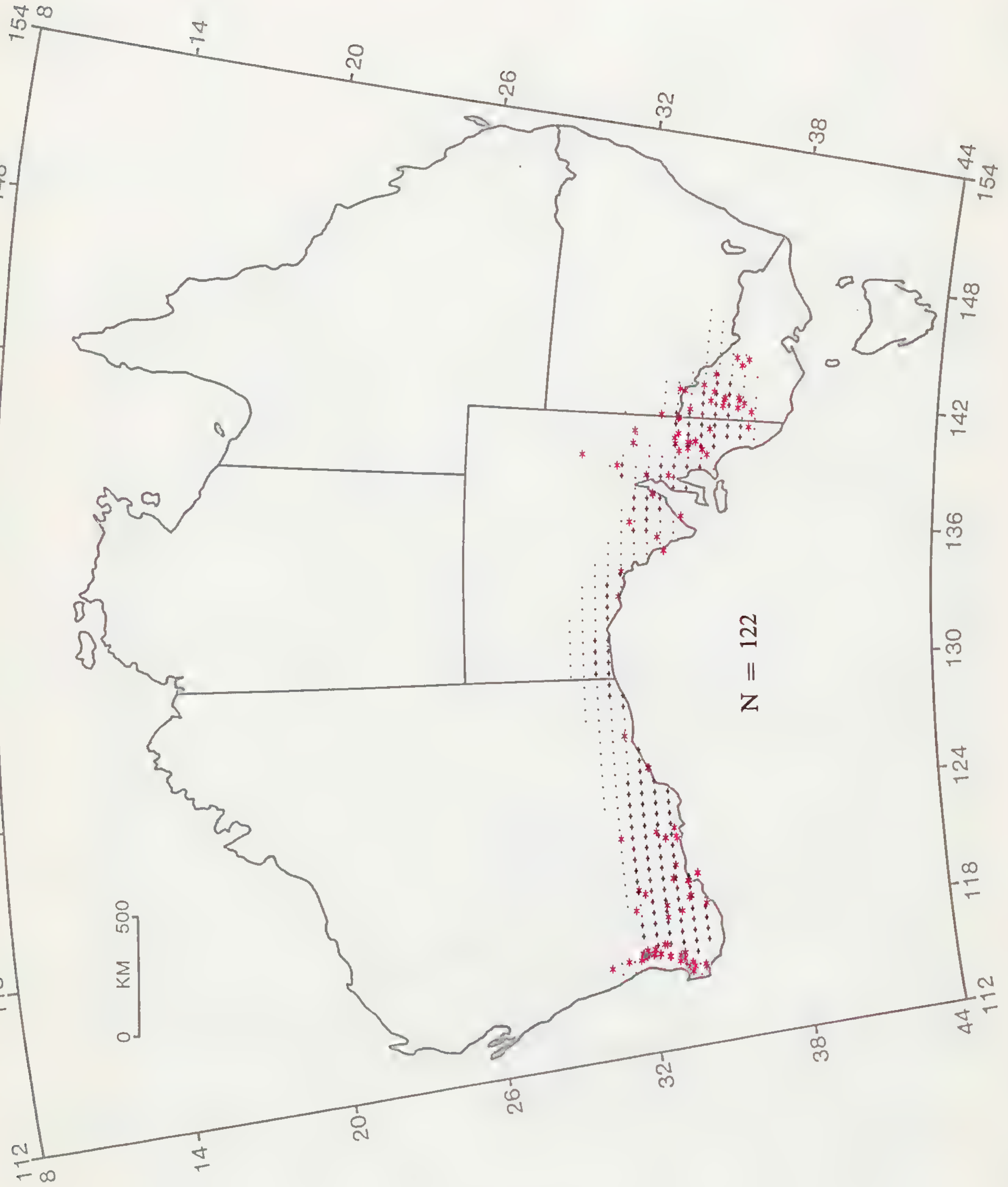
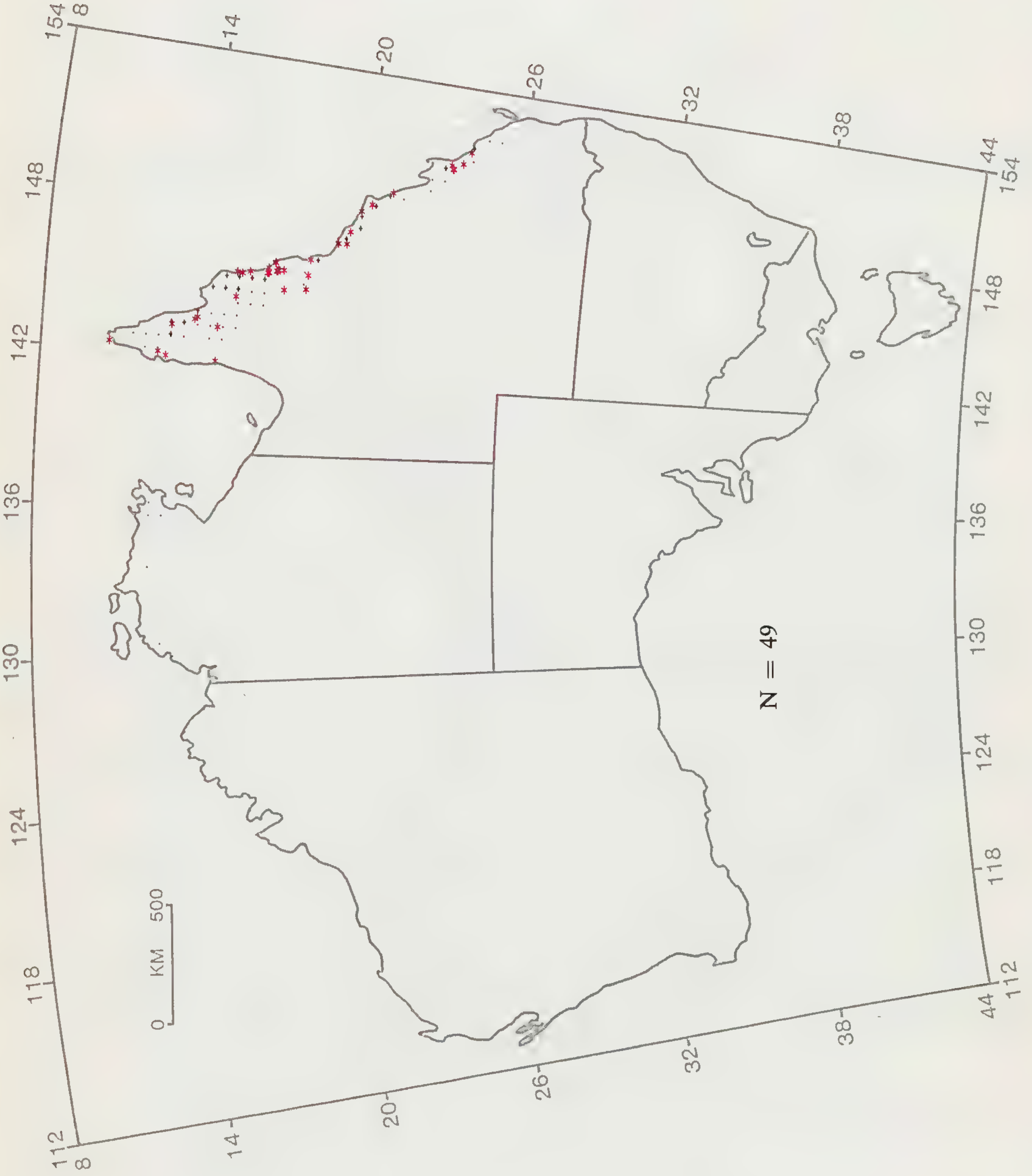
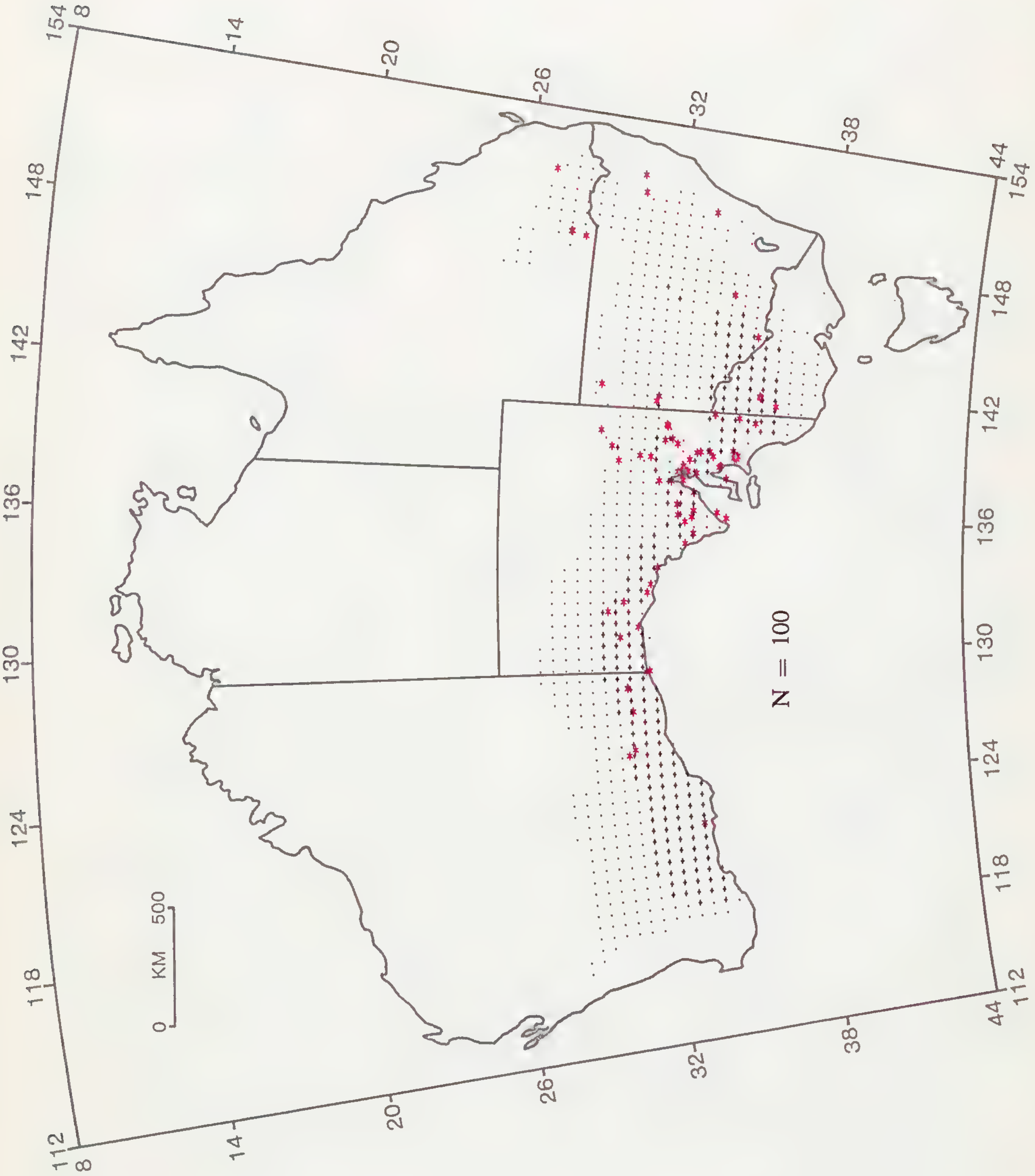
14
20
26
32
38
44
112
118
124
130
136
142
148
154

Map 74 Unechis nigriceps

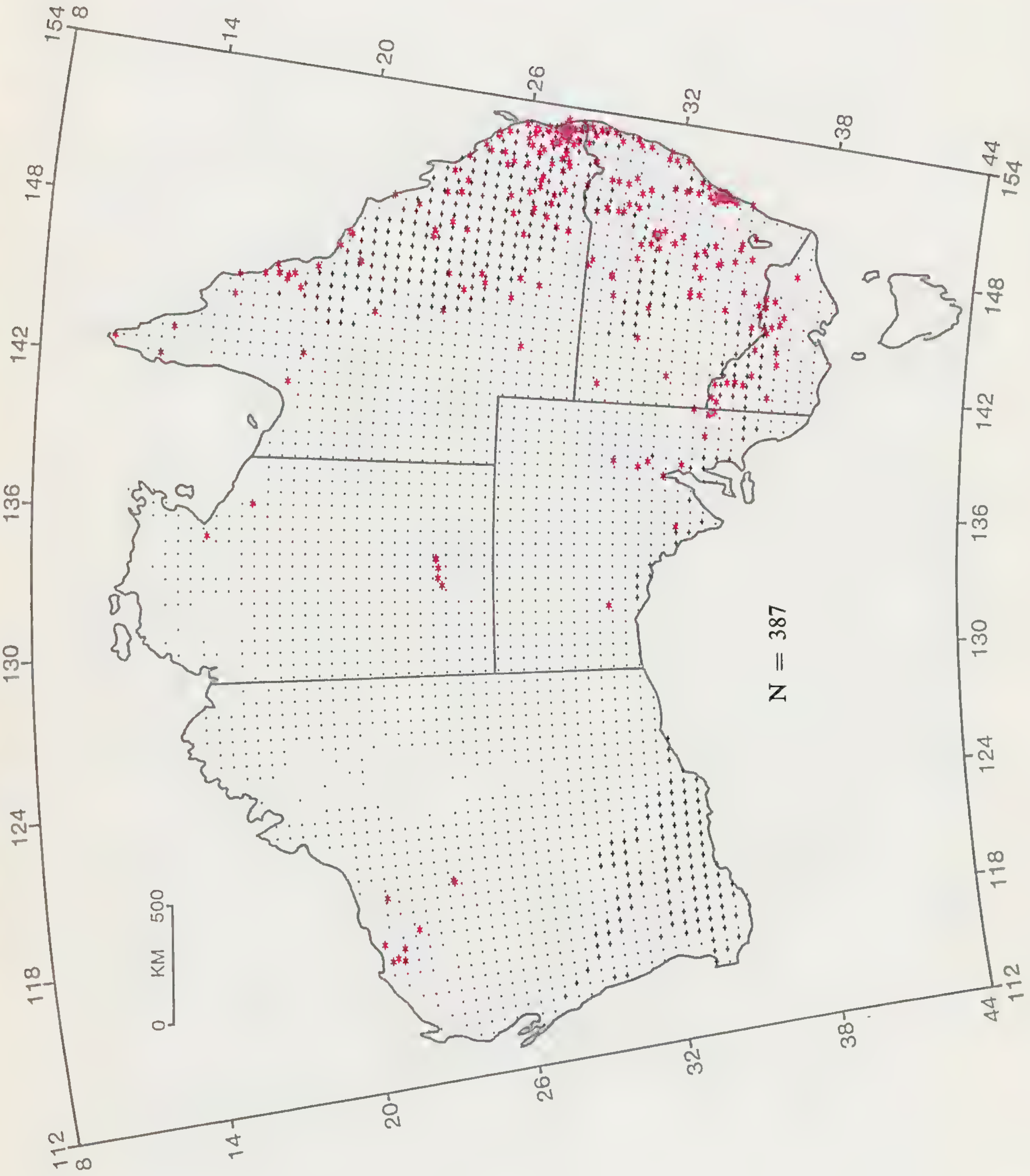



N = 49
0 KM 500
8
14
20
26
32
38
44
112
118
124
130
136
142
148
154

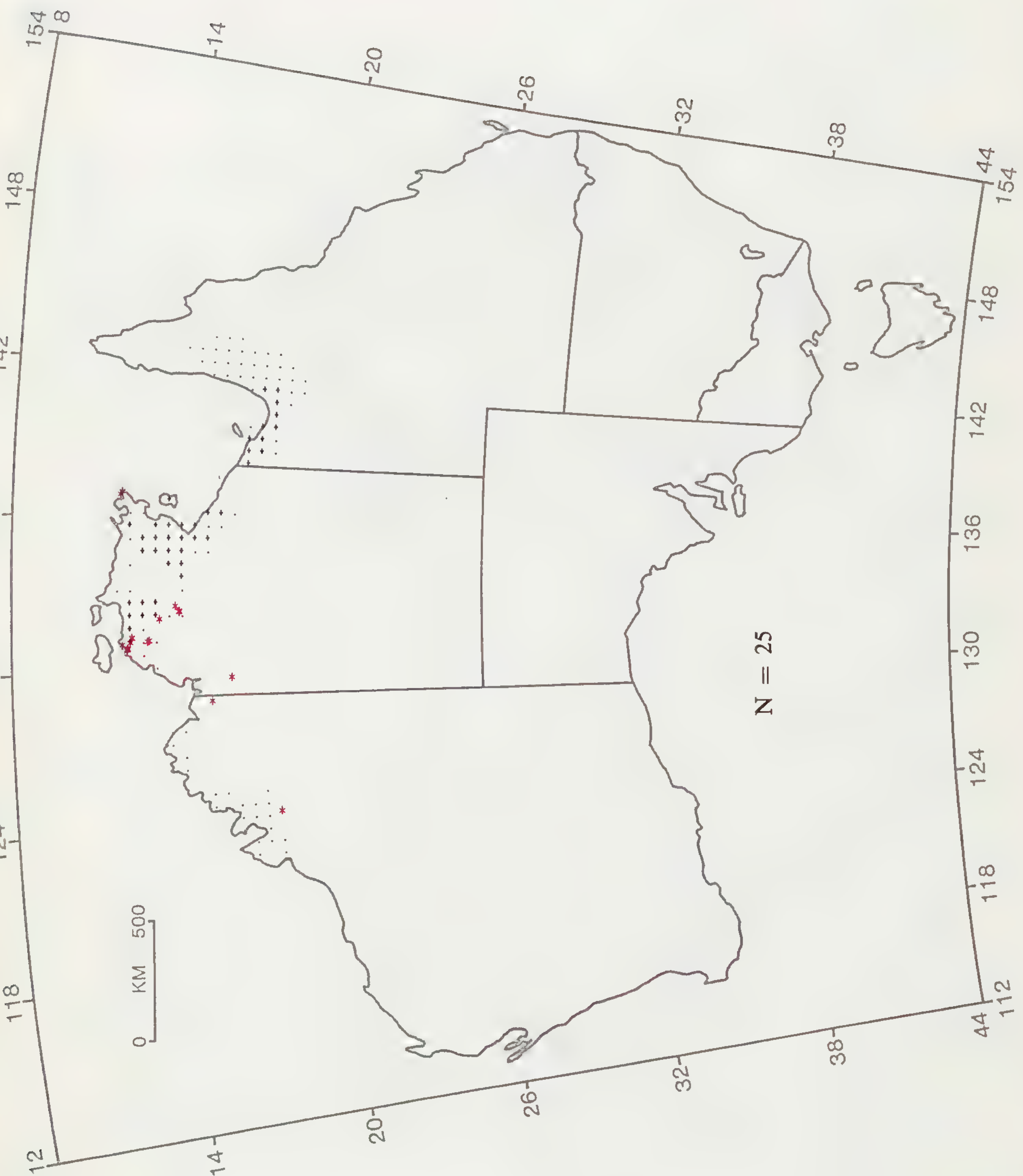
Map 76 Unechis spectabilis

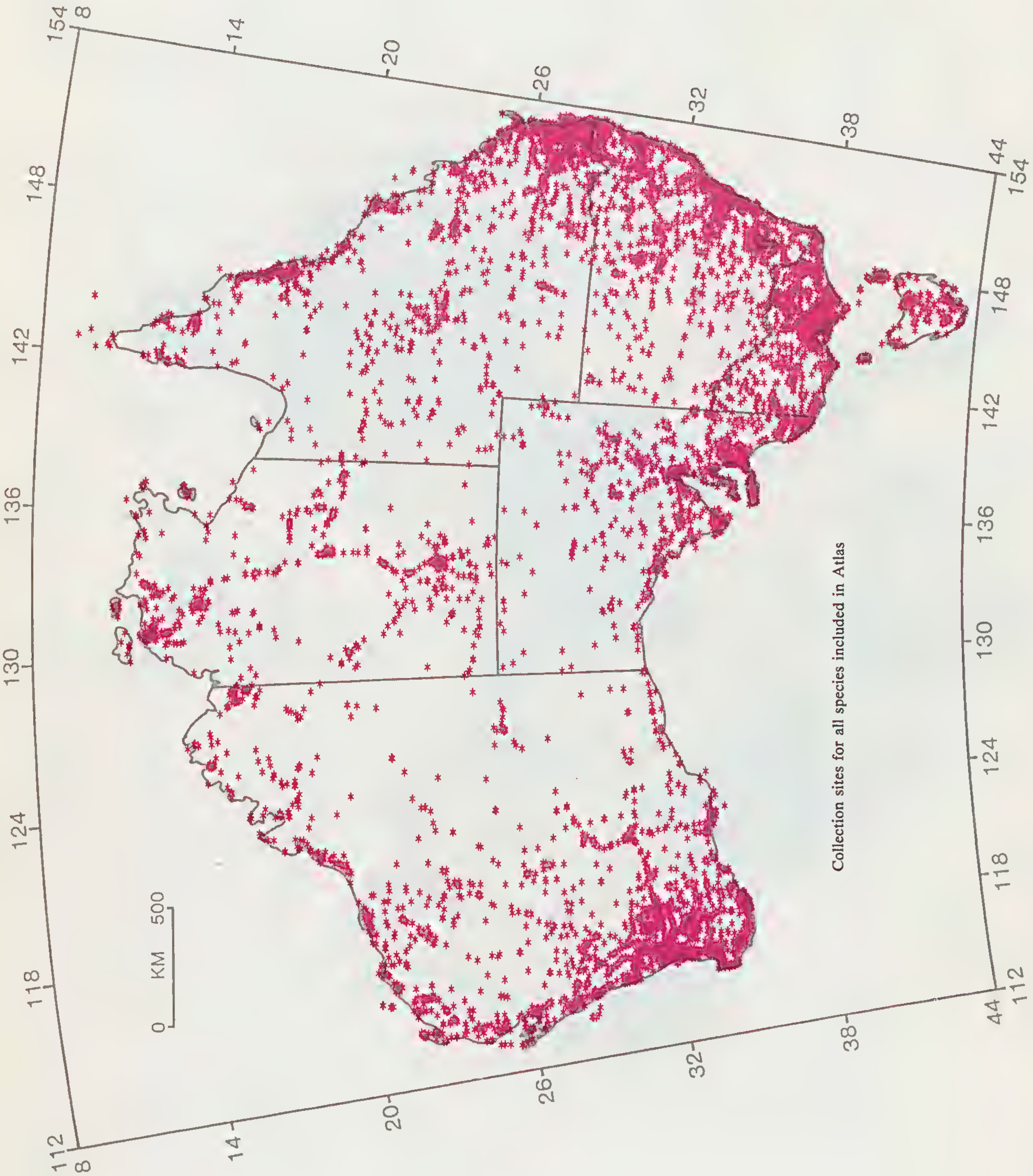


Vermicella annulata **Map 77**

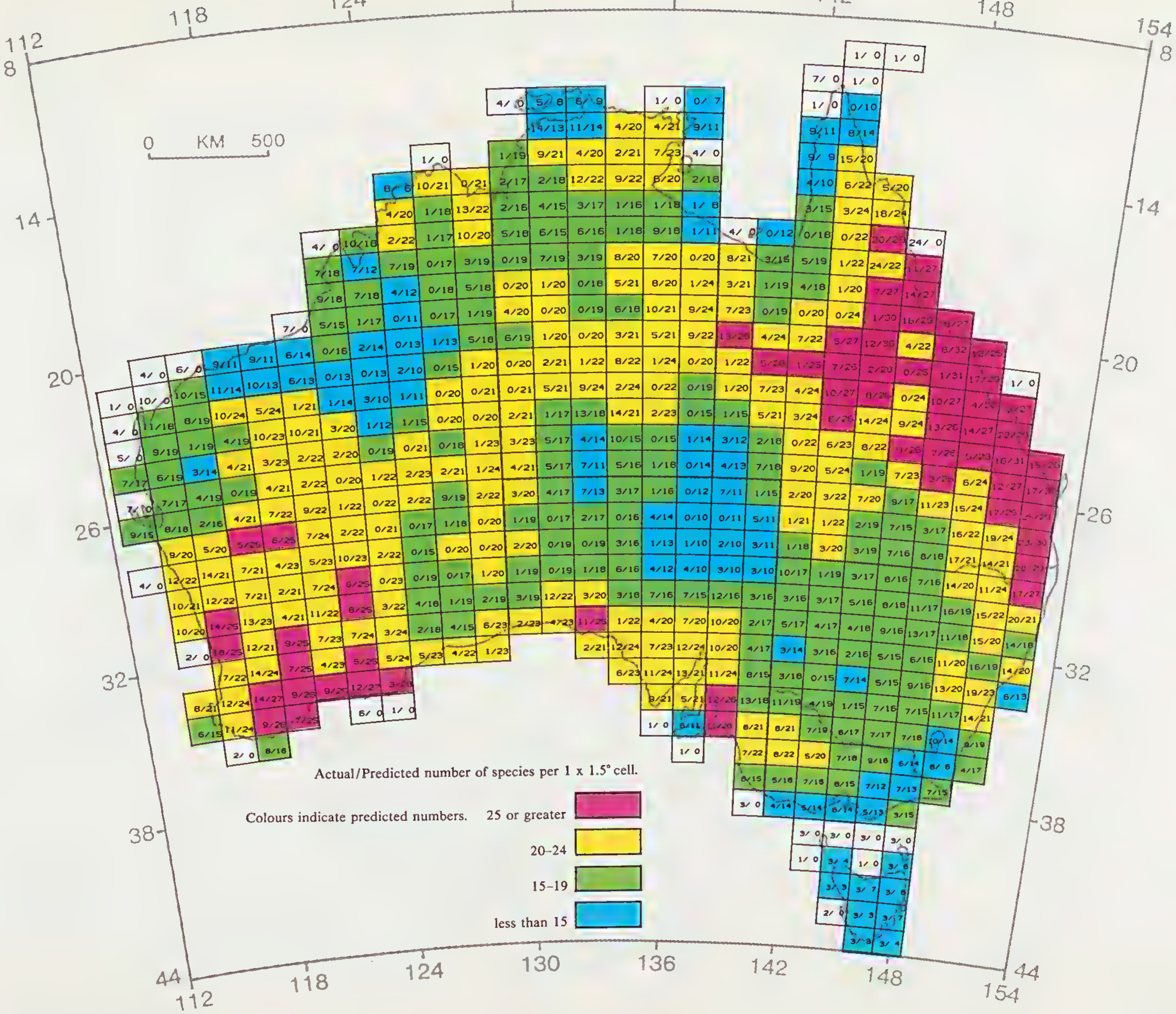


Map 78 Vermicella multifasciata





Collection sites for all species included in Atlas



Actual/Predicted number of species per 1 x 1.5° cell.

Colours indicate predicted numbers.
- 🟥 25 or greater
- 🟨 20–24
- 🟩 15–19
- 🟦 less than 15

Collection sites for all species included in atlas

CLIMATE PROFILES

The climate profiles used in the BIOCLIM predictions are listed below for each taxon.

The climate parameters are as follows:

1 annual mean temperature
2 minimum temperature of the coolest month
3 maximum temperature of the warmest month
4 annual temperature range (3 minus 2)
5 mean temperature of the wettest quarter (3 months)
6 mean temperature of the driest quarter
7 annual mean precipitation
8 precipitation of the wettest month
9 precipitation of the driest month
10 annual precipitation range (8 minus 9)
11 precipitation of the wettest quarter
12 precipitation of the driest quarter

All temperatures are in °C, precipitations in mm.

Values for the minima, 5 percentile, 95 percentile and maxima for each taxon are shown because these are the values used in the BIOCLIM predictions. Values for the means, standard deviations and 25 and 75 percentiles have also been determined and are available on application to the Director, Bureau of Flora and Fauna, GPO Box 1383, Canberra, A.C.T. 2601, Australia.

Appendix 3

PARAM	1	2	3	4	5	6	7	8	9	10	11	12
Acanthophis antarcticus												
Min	12.3	-0.4	24.1	11.3	8.4	7.2	151	16	0	7	45	4
5%	15.5	2.5	25.8	14.8	11.3	11.5	208	25	1	15	72	5
95%	27.0	17.8	38.1	29.6	30.3	24.8	1856	416	67	391	1142	229
Max	27.9	20.8	39.5	33.1	31.3	25.7	3830	734	103	631	1954	357
Acanthophis praelongus												
Min	19.8	8.5	28.5	13.5	23.0	16.3	321	74	1	72	198	4
5%	20.1	8.9	28.8	13.8	23.1	16.8	525	147	1	145	349	4
95%	27.7	18.8	38.3	26.8	29.6	25.6	2225	472	31	453	1354	104
Max	27.8	19.5	38.6	29.9	30.7	26.8	4027	775	103	672	2107	353
Acanthophis pyrrhus												
Min	18.3	3.3	31.6	22.2	12.4	14.3	161	22	0	11	58	3
5%	20.4	4.0	35.3	22.5	14.5	15.1	196	30	1	23	78	4
95%	27.1	13.2	40.2	33.7	31.8	26.3	481	130	8	128	326	30
Max	28.2	13.8	40.9	34.7	32.1	28.0	572	158	15	156	370	48
Austrelaps superbus												
Min	3.3	-6.4	15.8	12.9	0.2	3.6	300	42	10	10	124	33
5%	7.7	-2.0	20.2	15.3	3.5	6.0	435	60	14	21	167	48
95%	14.8	6.4	27.5	26.2	17.7	19.3	1644	189	87	112	521	276
Max	17.4	9.6	32.0	29.6	21.6	21.9	2682	324	122	221	898	407
Cacophis harriettae												
Min	16.7	1.8	25.9	14.2	20.8	12.4	629	89	0	56	246	0
5%	17.8	3.6	27.8	17.8	22.1	13.2	705	109	24	81	306	90
95%	22.6	11.6	31.5	26.0	26.2	19.6	1919	405	55	368	1036	197
Max	25.1	17.5	34.3	30.2	27.3	22.6	2403	491	61	460	1415	231
Cacophis krefftii												
Min	12.5	-1.5	24.1	14.1	15.2	9.5	620	88	11	59	235	40
5%	15.5	3.3	25.3	17.2	19.7	11.2	854	116	24	71	339	83
95%	23.9	13.5	31.6	24.6	26.6	21.7	2222	471	73	419	1296	245
Max	25.0	17.5	33.3	26.9	27.3	22.4	4192	825	106	720	2182	333
Cacophis squamulosus												
Min	12.8	-1.6	24.1	17.5	14.9	7.5	620	95	11	41	243	40
5%	15.1	0.5	25.3	18.4	15.4	10.2	894	110	32	52	303	118
95%	20.5	8.9	30.7	26.1	24.7	17.6	1818	273	73	207	793	248
Max	24.0	14.1	33.0	27.6	27.1	22.9	3116	639	92	604	1656	340
Cryptophis nigrescens												
Min	10.5	-1.7	22.2	14.2	6.0	5.7	384	49	2	15	140	11
5%	12.6	0.1	24.8	17.7	10.4	8.2	662	70	26	23	198	90
95%	23.0	12.1	32.6	27.1	26.5	20.9	1950	411	73	380	1159	250
Max	25.9	17.9	35.4	31.8	27.7	24.4	3824	769	95	674	2030	340
Cryptophis pallidiceps												
Min	25.2	9.3	32.3	12.0	27.6	20.2	772	196	1	196	515	4
5%	26.3	12.2	32.4	12.0	27.8	22.1	874	211	1	210	571	4
95%	27.9	19.9	37.6	25.2	29.6	25.6	1563	385	2	384	1000	14
Max	28.6	20.3	38.9	26.5	30.7	25.7	1565	385	3	384	1002	15
Demansia atra												
Min	17.4	4.9	27.5	11.3	21.6	13.0	625	148	0	121	409	0
5%	20.2	8.8	29.1	13.7	24.1	16.4	732	172	1	152	459	4
95%	27.8	19.4	38.6	25.4	30.3	25.5	1875	448	43	443	1204	151
Max	28.6	20.8	39.5	27.5	31.3	25.7	3553	692	100	592	1811	332
Demansia olivacea												
Min	21.2	4.8	32.0	12.1	16.6	15.4	217	43	0	39	100	3
5%	21.6	7.8	33.0	14.6	17.3	19.0	247	49	0	48	124	4
95%	28.4	19.6	40.2	30.0	31.5	27.4	1565	375	4	374	1002	19
Max	28.8	20.5	40.9	32.9	32.0	27.9	1619	385	18	384	1020	65
Demansia papuensis												
Min	25.8	11.1	32.4	12.1	27.9	21.3	713	174	1	173	467	4
5%	25.8	11.1	32.4	12.1	27.9	21.3	713	174	1	173	467	4
95%	27.8	19.5	38.8	25.0	30.7	25.6	1351	383	2	382	952	13
Max	28.6	20.3	38.9	27.4	30.7	25.7	1564	385	2	384	1002	14
Demansia psammophis												
Min	11.9	-1.4	23.5	11.8	6.7	9.0	110	12	0	6	33	3
5%	16.0	2.9	26.2	19.2	11.4	12.1	188	22	1	12	61	7
95%	25.3	12.8	38.6	32.3	30.5	25.0	1596	261	65	217	711	226
Max	28.5	20.6	40.9	34.6	32.0	27.6	2414	482	80	435	1354	277

PARAM	1	2	3	4	5	6	7	8	9	10	11	12
Demansia simplex												
Min	26.4	11.6	35.2	19.3	28.6	21.8	830	212	1	211	572	4
5%	26.4	11.6	35.2	19.3	28.6	21.8	830	212	1	211	572	4
95%	27.5	15.1	37.5	25.1	29.5	25.0	1255	328	2	326	887	15
Max	28.3	16.1	38.6	25.2	30.3	25.5	1274	333	2	332	902	15
Demansia torquata												
Min	19.1	2.5	29.3	13.3	23.5	13.3	162	24	0	14	66	0
5%	20.5	5.2	30.6	14.1	25.1	14.6	236	46	1	41	125	8
95%	26.7	17.5	38.9	31.4	30.8	23.6	1942	433	26	407	1170	96
Max	27.2	18.7	39.3	33.2	31.2	24.8	2234	478	38	453	1353	125
Denisonia devisi												
Min	17.8	1.8	31.5	27.3	23.6	11.6	253	35	3	18	103	17
5%	18.2	2.5	32.5	28.4	25.0	11.8	305	43	5	20	124	23
95%	23.9	7.8	37.3	31.9	28.8	18.8	613	96	33	83	253	108
Max	24.9	9.5	38.8	32.5	30.3	20.3	714	136	39	133	358	134
Denisonia fasciata												
Min	15.9	4.5	30.9	22.4	10.4	18.0	190	22	1	10	65	3
5%	17.5	4.7	33.2	24.2	11.8	18.6	202	27	1	15	75	5
95%	25.9	13.0	39.4	32.2	31.1	26.1	340	70	14	65	189	44
Max	26.8	13.9	40.9	32.3	31.8	26.6	479	86	17	78	236	55
Denisonia maculata												
Min	20.6	5.5	30.8	19.3	25.6	15.6	519	92	18	74	245	58
5%	20.9	6.1	31.1	20.6	25.7	16.2	601	101	18	77	292	65
95%	22.2	10.3	33.8	27.1	27.3	18.0	959	187	24	165	501	85
Max	22.5	11.5	35.0	29.0	27.8	18.4	1282	242	32	210	652	111
Denisonia punctata												
Min	21.2	3.3	34.3	16.8	28.1	14.9	152	25	0	20	57	3
5%	22.3	4.7	36.1	21.9	28.4	16.1	250	47	1	41	118	4
95%	28.2	15.2	40.2	32.9	31.8	27.6	981	226	7	224	631	28
Max	28.5	18.1	40.9	34.6	32.0	27.9	1526	340	9	338	963	35
Drysdalia coronata												
Min	12.6	1.4	25.6	16.0	6.1	19.2	293	34	1	18	92	9
5%	15.2	5.1	25.7	17.7	11.0	19.3	442	56	7	40	157	28
95%	18.1	9.1	31.0	23.7	14.6	23.5	1297	229	26	213	616	90
Max	19.6	10.5	32.6	26.3	16.3	24.5	1448	261	28	241	707	111
Drysdalia coronoides												
Min	2.7	-7.2	14.5	14.4	-1.3	4.6	427	50	14	17	139	46
5%	5.7	-3.6	17.7	15.6	1.8	7.8	534	65	29	20	177	101
95%	14.6	6.2	27.2	26.6	18.3	19.3	2030	216	105	129	620	349
Max	17.4	7.5	30.3	30.0	20.8	20.8	2834	334	132	225	935	437
Drysdalia mastersii												
Min	14.2	3.8	23.9	14.7	9.7	19.1	203	23	4	10	64	21
5%	14.8	3.9	24.3	14.8	10.0	19.7	204	23	4	11	66	21
95%	17.9	9.2	31.1	26.5	13.9	22.1	403	58	18	52	156	64
Max	17.9	9.5	31.4	27.5	15.9	22.8	558	78	19	61	228	65
Drysdalia rhodogaster												
Min	11.4	-0.6	23.3	17.4	14.7	6.8	636	66	41	18	176	140
5%	12.0	-0.3	23.5	17.8	14.9	6.8	805	87	48	32	240	147
95%	16.9	6.7	27.1	26.3	20.6	13.3	1433	178	77	106	489	237
Max	17.4	7.3	28.1	27.2	21.1	17.2	1584	196	78	129	548	249
Echiopsis curta												
Min	12.6	1.4	24.8	15.7	6.1	11.1	110	12	4	6	33	20
5%	14.9	3.9	25.7	18.1	10.2	19.3	209	24	4	14	69	23
95%	19.2	9.2	33.6	28.2	15.8	23.7	1035	202	22	192	526	78
Max	20.3	10.4	36.3	31.0	27.1	25.2	1314	242	27	228	644	96
Elapognathus minor												
Min	15.3	6.5	25.6	18.1	11.5	19.2	756	110	7	89	299	29
5%	15.3	6.5	25.6	18.1	11.5	19.2	756	110	7	89	299	29
95%	18.2	8.8	30.3	21.5	13.7	23.3	1354	243	27	225	655	97
Max	18.2	9.0	31.2	23.1	14.1	23.7	1405	255	27	235	684	98
Furina diadema												
Min	12.0	-1.1	24.7	17.6	7.0	6.9	119	12	5	5	32	19
5%	14.6	0.4	26.3	19.9	15.5	11.0	316	38	12	17	104	43
95%	21.9	8.6	35.1	31.3	27.2	19.9	1268	181	66	149	501	224
Max	23.9	13.6	39.2	33.3	29.3	22.2	1968	394	77	363	1085	273

Appendix 3

PARAM	1	2	3	4	5	6	7	8	9	10	11	12
Furina ornata												
Min	16.6	1.1	29.4	11.8	11.4	9.9	174	18	0	8	51	1
5%	20.5	4.4	31.6	14.4	24.2	15.2	241	35	1	29	101	4
95%	28.0	19.5	40.0	32.0	31.5	26.2	1600	401	19	397	1084	66
Max	29.0	20.5	41.6	34.1	32.1	27.8	2232	472	38	453	1354	130
Glyphodon barnardi												
Min	21.6	6.9	30.7	13.6	25.9	16.7	354	73	0	68	202	0
5%	21.6	6.9	30.7	13.6	25.9	16.7	354	73	0	68	202	0
95%	25.7	18.4	37.8	27.3	29.2	24.3	1045	267	20	267	769	72
Max	26.3	18.6	37.8	30.9	29.9	24.8	1683	410	26	395	1111	96
Glyphodon dunmalli												
Min	17.9	2.2	30.1	18.6	23.5	12.5	570	86	22	58	222	74
5%	17.9	2.2	30.1	18.6	23.5	12.5	570	86	22	58	222	74
95%	22.1	10.2	33.7	29.5	26.4	17.8	976	176	30	147	468	108
Max	22.3	12.0	34.1	30.2	26.8	18.5	1022	187	32	162	471	109
Glyphodon tristis												
Min	23.0	12.0	31.5	10.0	25.4	21.3	1167	272	0	255	747	3
5%	23.7	14.4	31.5	10.0	25.5	21.8	1175	274	1	257	776	4
95%	26.5	21.5	33.8	17.9	27.6	25.7	1925	450	23	445	1215	83
Max	26.7	21.6	34.2	20.8	27.7	25.9	2132	485	30	455	1285	104
Hemiaspis damelii												
Min	16.1	2.2	29.0	20.8	9.0	12.1	292	29	14	8	81	59
5%	17.7	2.4	30.4	22.0	11.0	12.3	395	43	22	11	124	72
95%	21.9	8.9	34.5	31.5	26.6	17.7	913	175	32	152	439	113
Max	22.1	9.9	34.6	31.5	27.3	23.5	1840	261	67	194	719	243
Hemiaspis signata												
Min	11.2	-1.7	22.3	14.5	15.0	6.3	487	62	6	20	172	22
5%	13.2	-0.4	25.1	18.1	15.5	9.7	731	101	27	56	279	99
95%	21.9	11.2	32.1	27.0	26.3	18.1	1919	330	73	273	904	245
Max	25.1	17.0	34.7	31.5	27.1	24.2	3570	824	93	757	1866	317
Hoplocephalus bitorquatus												
Min	10.6	-1.2	23.6	14.5	15.3	10.3	453	55	1	18	155	5
5%	16.8	1.9	27.3	18.9	20.9	12.3	509	70	19	38	185	68
95%	22.3	11.2	34.2	31.1	27.2	18.5	1282	209	55	184	578	194
Max	24.5	16.9	36.2	31.5	27.9	21.8	3116	520	92	434	1501	340
Hoplocephalus bungaroides												
Min	12.0	-0.2	24.1	18.4	14.2	6.9	674	78	33	24	222	109
5%	12.1	0.2	24.6	19.1	14.9	6.9	777	80	51	41	226	170
95%	17.4	6.8	26.7	25.9	21.2	17.3	1338	157	70	95	436	243
Max	17.5	6.9	28.9	26.5	21.8	17.4	1563	189	78	120	540	249
Hoplocephalus stephensii												
Min	13.9	0.9	24.1	17.9	18.3	9.7	645	77	26	32	218	91
5%	14.8	1.6	24.2	18.7	19.1	11.1	662	99	32	54	259	108
95%	20.1	8.8	30.1	27.0	24.0	16.9	1852	280	76	230	825	253
Max	20.2	9.6	30.5	28.3	24.2	18.2	3116	520	93	427	1501	340
Neelaps bimaculatus												
Min	16.0	4.6	26.6	19.8	10.5	18.2	168	20	1	11	45	10
5%	16.6	4.9	29.6	20.5	11.5	18.3	212	27	4	15	75	17
95%	20.3	9.0	35.5	29.2	16.8	23.8	895	194	13	187	516	42
Max	22.0	9.2	38.1	31.2	26.4	25.1	919	200	20	193	521	63
Neelaps calonotus												
Min	16.8	5.6	29.1	20.6	11.3	22.4	452	90	6	81	243	23
5%	17.8	7.1	29.5	21.0	13.0	22.8	687	151	6	143	395	25
95%	18.5	9.0	31.3	25.2	14.5	23.8	887	188	9	180	504	33
Max	19.2	9.4	34.6	28.5	14.6	24.4	1058	217	10	207	591	39
Notechis ater												
Min	3.9	-3.7	14.6	14.5	-0.6	8.9	383	53	5	17	145	25
5%	9.1	1.4	19.5	16.5	5.9	11.7	484	64	7	24	177	29
95%	18.2	8.8	31.2	25.1	13.8	23.6	2061	250	93	215	683	334
Max	19.1	10.4	33.4	27.5	14.8	24.2	2629	316	122	261	847	396
Notechis scutatus												
Min	6.1	-2.7	18.4	15.7	1.3	3.6	258	26	16	9	74	52
5%	10.9	-1.2	23.2	18.5	7.0	7.1	436	48	24	16	136	76
95%	18.5	7.1	30.8	28.4	22.3	20.8	1645	237	74	183	669	250
Max	20.4	10.1	33.2	29.7	24.3	23.2	3116	520	94	427	1501	340

PARAM	1	2	3	4	5	6	7	8	9	10	11	12
Oxyuranus scutellatus												
Min	18.1	4.7	28.3	12.1	22.4	13.5	698	121	0	90	348	0
5%	19.6	6.4	28.9	13.5	24.1	15.2	874	135	1	101	372	6
95%	27.2	19.1	35.3	24.0	28.2	25.3	2301	490	55	461	1393	192
Max	27.8	20.2	36.7	25.9	29.1	25.5	4027	775	105	672	2107	369
Parademansia microlepidota												
Min	17.3	4.3	33.0	28.7	14.2	15.2	128	19	4	11	50	19
5%	22.2	5.8	38.6	31.3	29.3	15.3	129	19	4	14	50	19
95%	24.2	7.1	39.4	33.3	30.4	18.2	270	48	8	43	128	29
Max	24.5	7.6	39.5	33.6	30.4	21.2	278	57	16	53	155	58
Pseudechis australis												
Min	15.1	1.1	27.6	12.0	8.8	9.5	117	12	0	5	32	0
5%	17.2	3.1	30.8	15.3	11.9	13.2	187	23	1	12	62	4
95%	27.6	18.4	39.3	33.3	31.2	25.6	1460	339	26	336	949	89
Max	29.1	20.3	40.9	34.6	32.0	27.9	2985	667	59	608	1741	195
Pseudechis butleri												
Min	20.1	5.3	36.0	29.8	14.3	16.8	199	28	2	20	75	12
5%	20.1	5.3	36.0	29.8	14.3	16.8	199	28	2	20	75	12
95%	21.9	6.9	38.1	31.7	29.0	23.6	283	50	8	42	129	28
Max	23.2	6.9	39.3	32.4	30.4	23.6	287	52	8	44	133	29
Pseudechis colletti												
Min	20.6	4.1	34.9	28.0	27.4	14.3	385	68	3	49	192	13
5%	21.1	4.7	35.0	28.0	27.5	15.2	393	70	3	59	196	15
95%	25.3	9.7	38.0	30.4	29.8	20.5	483	110	19	107	282	66
Max	25.7	10.2	38.2	31.0	30.1	20.8	505	112	22	109	284	75
Pseudechis guttatus												
Min	13.8	-0.6	26.4	18.1	8.2	9.7	410	40	23	12	112	84
5%	16.0	1.0	28.7	22.7	21.1	11.2	459	49	27	17	140	91
95%	20.0	6.8	33.7	30.9	25.8	16.9	940	150	39	113	404	131
Max	21.9	11.5	34.6	31.6	26.9	19.8	1099	198	43	169	501	149
Pseudechis porphyriacus												
Min	9.8	-2.4	20.8	14.5	6.0	5.0	181	19	6	9	55	23
5%	12.3	-0.5	24.5	18.3	8.2	9.1	407	48	16	18	135	54
95%	21.3	10.2	32.5	29.3	25.5	21.7	1959	406	71	366	1080	238
Max	25.4	17.8	34.6	31.7	27.1	24.5	3378	823	84	769	2049	303
Pseudonaja affinis												
Min	14.7	4.3	25.7	16.2	10.2	18.1	196	23	6	9	63	23
5%	15.4	4.6	27.1	19.1	10.7	20.1	318	43	7	33	127	28
95%	18.2	9.0	32.3	27.6	14.2	23.7	1161	235	19	225	641	63
Max	18.8	10.3	34.9	29.3	24.4	24.3	1447	276	27	264	742	96
Pseudonaja guttata												
Min	21.3	4.9	33.6	25.8	27.2	15.5	127	19	1	14	49	8
5%	22.2	5.9	34.7	27.0	27.6	16.1	200	38	2	29	94	9
95%	25.8	10.4	39.1	32.8	30.8	21.1	515	112	15	109	289	53
Max	26.3	11.3	39.5	33.2	31.2	21.9	627	127	21	124	337	69
Pseudonaja ingrami												
Min	24.1	6.7	37.5	26.9	29.7	17.8	236	46	1	41	125	9
5%	24.2	7.0	37.9	27.0	30.0	17.8	238	47	1	42	125	9
95%	26.2	11.1	39.2	32.1	30.9	21.9	479	117	4	115	309	18
Max	28.0	12.3	39.6	32.6	31.4	24.4	597	155	5	154	399	22
Pseudonaja modesta												
Min	15.6	2.2	26.6	15.3	10.1	10.9	87	11	0	5	32	4
5%	17.3	4.2	32.6	23.7	11.9	13.5	162	21	1	11	51	5
95%	26.9	13.1	39.9	33.4	31.4	25.5	673	165	13	164	437	44
Max	29.1	18.4	41.6	34.6	32.1	27.9	1098	286	20	286	751	63
Pseudonaja nuchalis												
Min	14.8	2.4	25.4	12.0	8.2	10.5	107	11	0	4	29	2
5%	16.5	3.6	30.2	18.4	11.4	13.4	150	19	1	9	49	5
95%	27.3	16.4	39.3	33.7	30.9	25.6	1181	276	18	276	757	60
Max	29.0	20.3	41.6	35.0	32.1	28.0	1655	401	38	401	1084	136
Pseudonaja textilis												
Min	9.6	-1.9	22.3	13.5	5.6	4.5	127	14	1	6	40	4
5%	12.9	0.0	25.2	18.4	8.0	9.9	200	24	6	11	66	25
95%	23.0	9.3	36.9	31.3	28.4	22.4	1381	223	63	179	629	213
Max	27.4	18.7	39.6	34.6	30.9	24.9	2222	471	93	444	1374	288

Appendix 3

PARAM	1	2	3	4	5	6	7	8	9	10	11	12
Rhinoplocephalus bicolor												
Min	15.0	4.8	25.7	16.2	11.0	19.2	441	56	10	39	163	37
5%	15.1	5.4	25.7	18.1	11.1	19.3	456	65	11	47	184	40
95%	16.4	8.5	28.4	21.9	13.6	20.8	1343	240	27	215	640	93
Max	16.7	10.4	30.6	25.8	14.5	21.9	1367	242	28	229	659	98
Simoselaps anomalus												
Min	18.85	2.4	33.5	21.1	23.6	12.2	152	21	0	16	52	3
5%	19.8	2.9	34.7	21.9	26.4	13.1	159	27	0	21	61	3
95%	27.3	13.4	40.1	34.5	31.6	25.5	555	162	11	160	387	36
Max	28.4	16.1	40.2	34.6	32.0	27.7	603	170	12	170	424	37
Simoselaps approximans												
Min	17.3	4.8	33.5	21.1	12.2	19.1	193	27	1	24	78	4
5%	17.3	4.8	33.5	21.1	12.2	19.1	193	27	1	24	78	4
95%	27.3	13.7	39.6	32.3	31.8	26.7	454	120	4	119	305	19
Max	27.3	13.9	40.5	32.4	32.0	27.7	579	165	8	163	403	28
Simoselaps australis												
Min	12.5	-3.2	24.7	14.5	6.3	8.6	125	13	4	5	35	15
5%	14.8	1.3	26.4	21.2	11.9	11.1	154	18	9	7	50	31
95%	23.0	8.6	36.1	31.2	28.0	21.2	1001	175	40	142	475	138
Max	24.5	16.9	39.6	33.3	30.1	23.8	2222	471	46	433	1352	157
Simoselaps bertholdi												
Min	14.6	2.9	24.9	15.8	10.0	12.9	119	12	0	5	32	4
5%	15.9	4.6	28.9	20.7	11.1	17.6	168	20	3	11	53	11
95%	22.3	9.1	37.8	31.1	28.5	24.0	889	194	13	186	506	44
Max	25.2	13.3	40.7	34.6	31.7	25.9	1405	255	21	236	685	83
Simoselaps fasciolatus												
Min	15.8	2.4	29.5	20.8	9.0	12.0	128	17	0	10	48	9
5%	17.1	3.1	30.0	21.1	11.4	13.2	156	20	1	11	53	9
95%	22.1	9.6	38.4	32.7	29.5	24.1	860	184	14	176	492	52
Max	26.6	11.1	38.8	34.1	30.1	25.1	910	194	17	185	519	56
Simoselaps incinctus												
Min	20.9	3.6	36.4	22.1	27.9	14.5	191	27	2	21	74	7
5%	20.9	3.6	36.4	22.1	27.9	14.5	191	27	2	21	74	7
95%	25.2	10.6	38.1	34.1	29.9	19.9	414	90	9	86	244	36
Max	26.9	14.3	38.3	34.4	29.9	23.0	693	172	14	170	494	46
Simoselaps littoralis												
Min	17.8	8.1	29.6	21.0	14.6	22.2	233	44	0	43	112	3
5%	19.1	8.2	31.6	22.4	15.7	22.4	239	52	0	52	125	4
95%	24.1	12.7	35.8	26.4	19.9	25.6	594	147	4	143	356	22
Max	24.6	13.2	36.4	27.4	26.0	26.1	846	189	7	182	490	27
Simoselaps semifasciatus												
Min	15.2	2.9	25.7	14.9	10.6	12.3	145	19	0	9	49	0
5%	16.8	4.6	30.1	20.7	11.3	16.0	195	29	1	15	80	6
95%	27.8	14.6	38.9	31.8	31.1	25.1	1000	216	12	213	582	43
Max	29.1	19.5	39.4	34.6	31.6	27.6	1563	385	22	384	1001	75
Simoselaps warro												
Min	22.0	11.0	30.6	13.7	24.8	18.1	868	225	0	198	582	3
5%	22.3	11.2	31.6	13.9	25.2	19.3	873	237	1	233	626	4
95%	26.6	18.8	34.2	21.3	27.7	24.6	1611	438	19	429	1179	69
Max	27.3	19.5	35.5	21.4	28.4	24.6	2043	446	28	446	1288	109
Suta suta												
Min	13.5	0.0	27.2	14.5	7.0	10.6	110	11	1	5	30	5
5%	15.8	2.5	30.4	21.5	9.7	11.7	148	19	2	8	48	9
95%	25.8	12.0	39.0	33.9	30.6	23.2	761	175	34	173	494	113
Max	27.6	18.8	39.6	34.6	31.1	25.1	2088	446	42	446	1272	140
Tropidechis carinatus												
Min	14.4	1.6	24.1	14.5	18.9	9.8	548	82	17	58	221	59
5%	15.4	3.2	24.6	18.1	19.3	11.1	903	130	30	96	354	100
95%	20.5	10.0	30.3	25.1	24.4	19.1	1882	338	65	315	969	243
Max	24.5	16.9	32.9	28.4	27.0	22.2	3542	714	92	631	1861	340
Unechis boschmai												
Min	16.9	1.8	27.0	13.4	21.5	12.4	492	70	1	43	185	8
5%	17.3	2.2	28.2	14.5	22.2	12.5	526	85	2	63	225	9
95%	24.5	15.2	34.7	29.6	27.3	21.9	1649	369	33	354	1058	114
Max	27.3	18.6	37.3	31.2	29.6	24.8	2234	472	38	434	1353	124

PARAM	1	2	3	4	5	6	7	8	9	10	11	12
Unechis dwyeri												
Min	10.0	-2.2	22.5	19.9	5.7	6.8	302	30	19	7	81	62
5%	12.3	-1.1	25.0	24.1	7.4	9.5	364	36	23	9	102	77
95%	20.2	4.4	34.5	31.0	26.6	22.4	865	114	52	83	322	160
Max	20.8	8.1	35.2	31.8	27.7	24.5	1840	261	67	194	719	243
Unechis flagellum												
Min	11.0	-0.5	23.8	16.7	5.6	6.5	315	43	11	15	125	37
5%	12.0	-0.3	24.9	18.5	7.2	6.8	373	50	13	16	142	43
95%	15.4	6.4	29.8	27.2	14.9	20.8	883	103	48	70	297	155
Max	15.9	7.6	31.3	28.2	18.3	22.3	1056	129	62	81	364	195
Unechis gouldii												
Min	15.0	4.3	25.8	18.3	10.1	18.3	197	22	4	10	62	14
5%	15.5	4.5	28.6	20.9	10.5	20.4	267	32	7	16	91	28
95%	18.9	8.9	34.3	29.1	14.0	23.9	1077	223	17	213	598	56
Max	21.8	9.3	37.9	30.3	16.1	24.8	1306	281	26	269	732	94
Unechis monachus												
Min	17.9	2.9	31.5	23.7	12.3	13.1	156	20	0	9	45	6
5%	18.4	3.8	32.6	25.7	12.8	13.4	184	21	1	11	57	10
95%	24.9	10.0	39.6	32.3	30.9	24.6	368	88	12	84	217	41
Max	26.3	13.4	41.5	33.7	31.9	26.1	485	125	13	121	301	42
Unechis nigriceps												
Min	13.7	1.6	26.2	16.4	7.7	11.0	115	12	5	6	33	21
5%	14.5	3.2	27.0	19.4	9.0	18.3	142	14	6	6	41	28
95%	17.8	8.5	32.9	28.5	14.1	23.4	1091	227	21	216	606	70
Max	18.7	10.1	33.5	29.3	24.1	24.8	1295	270	27	258	740	96
Unechis nigrostriatus												
Min	20.0	8.4	29.0	12.0	23.3	16.3	718	168	0	146	433	4
5%	21.3	9.8	30.2	13.8	23.9	17.4	875	185	1	159	494	5
95%	26.4	18.5	34.1	21.4	27.5	24.6	2222	472	37	434	1353	115
Max	27.3	20.4	35.5	22.3	28.4	24.9	2400	542	39	503	1471	132
Unechis spectabilis												
Min	12.3	-1.4	24.8	15.7	7.9	7.1	133	15	5	6	42	20
5%	13.8	2.8	27.2	22.5	8.8	10.4	154	15	6	6	45	25
95%	18.7	6.6	33.2	30.1	25.3	23.8	547	76	27	53	219	86
Max	20.5	9.1	36.9	31.6	27.5	24.2	816	98	52	65	263	164
Vermicella annulata												
Min	11.7	-0.8	24.1	12.0	7.0	7.1	110	12	1	5	32	5
5%	15.0	1.8	26.4	18.7	9.5	11.4	243	28	4	11	78	16
95%	24.8	12.6	37.4	31.2	28.6	22.9	1587	267	65	244	748	223
Max	27.3	20.4	40.9	34.6	31.8	26.6	3116	520	93	473	1501	340
Vermicella multifasciata												
Min	26.6	12.2	32.9	14.5	27.6	22.4	523	156	1	155	367	4
5%	26.6	12.3	32.9	14.5	28.1	22.6	651	160	1	159	428	4
95%	27.8	19.5	38.9	25.2	30.4	25.7	1565	385	2	384	1001	8
Max	28.6	19.7	40.2	26.9	31.2	27.8	1567	385	3	384	1003	15

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